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GEOGRAPHIC SPECIATION IN TROPICAL ECHINOIDS

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The great importance of ecological factors in speciation is stressed by most recent students. Since the ecology of marine organisms is fundamentally different from that of such typical land animals as mammals, birds, land snails, and butterflies, one might expect modes of speciation in the oceans that differ completely from the typical geographic speciation of land animals. This possibility has been suggested repeatedly within recent years; yet a thorough study of speciation patterns in marine organisms has remained a desideratum.

Methodological difficulties. Speciation is the acquisition of reproductive isolation and of ecological compatibility by natural populations. There are several potential modes of speciation. How can one prove which of them has occurred in a particular case? Speciation is a slow historical process and can never be observed directly by an individual observer except in the case of polyploidy.

The student of speciation is thus in the same predicament as the archeologist, the geologist—and often the cytologist—all of whom study dynamic processes, which are fixed, so to speak, at definite, instantaneous, static levels. The method in all these sciences is the same. It consists in the reconstruction of a continuous series, by placing fixed stages into a correct chronological sequence. We must therefore ask: What are these fixed stages in the process of speciation? and: In what sequence should they be arranged?

On the basis of work on birds, butterflies, and other terrestrial animals, it has been found that the following phenomena, among others, can be interpreted as indicating geographic speciation.

(1) Geographic variation and the formation of polytypic species.

(2) The occurrence of geographical isolates and the existence of efficient extrinsic barriers limiting gene flow between these isolates.

(3) The occurrence of borderline cases, particularly the presence of allopatric populations that may be considered either species or subspecies.

(4) The occurrence of superspecies, that is of groups of allopatric species.

The object of the present investigation is to determine whether or not the four listed types of phenomena are sufficiently frequent among marine animals to indicate that they have the same speciation pattern as land animals.

Geographic variation among marine animals and the occurrence of polytypic species has been recorded by various authors. Döderlein, in particular, applied the poly-

typic species concept consistently from 1902 on. Rensch (1929, 1933, 1947) summarizes much of the literature, which indicates that polytypic species are of widespread occurrence among marine animals. The only attempt, known to me, to analyze a whole family or genus systematically is that of the Schilders (1939) who show that more than 50 per cent of the species of cowries (*Cypraea*) are polytypic. It appeared important to extend this line of work and to analyze some other marine groups to determine quantitatively the percentage of polytypic species and of borderline cases. The chief difficulty in this endeavor is that most groups of marine organisms are still far too poorly known to permit the kind of analysis that one can apply to birds or butterflies. There are, however, some exceptional groups that are fairly well known, one of them being the littoral echinoderms. We are particularly fortunate in having available for the echinoids a recently completed, thorough, and authoritative work: Mortensen's Monograph of the Echinoidea. This work proves to be an almost inexhaustible source of valuable information. The subsequent analysis is largely based on an evaluation of this work.

An analysis, like the proposed one, is valuable only if it is quantitative. It should include every species of a given taxonomic group that occurs in a circumscribed region. Since the deep sea species are still insufficiently known, it was decided to confine the present analysis to forms which occur in shallow water. The West Indies were chosen as a suitable area, since I had an opportunity to become familiar with living individuals in the waters around the Lerner Marine Biological Laboratory at Bimini, Bahamas. I am deeply indebted to Mr. M. Lerner and to Dr. Charles M. Breder of the Department of Fishes and Aquatic Biology at the American Museum of Natural History for the opportunity of a stay at Bimini and to Mr. and Mrs. Marshall B. Bishop for much assistance during my studies.

Dr. Norman D. Newell and Dr. Grace E. Pickford have kindly read the manuscript which has greatly benefited by their suggestions. I am also greatly indebted to Dr. Charles A. Vaurie for having drawn the distribution maps.

Speciation in the Shallow Water Sea Urchins of the West Indies

Although the student of sea urchins is more fortunate than most other workers on marine invertebrates by having available Mortensen's magnificent monograph of the echinoids, nevertheless most of the taxonomy is still essentially alpha taxonomy. Allopatric populations that are clearly distinct are generally ranked by Mortensen as full species, populations less clearly defined, as "varieties." Individual variants within populations are likewise recorded as "varieties." The term subspecies hardly occurs in the volumes. It is evident that many of the so-called "species" would be called subspecies in those branches of taxonomy where the polytypic species concept is consistently employed. Yet, so many of Mortensen's "species" are so obviously on the borderline between species and subspecies that vague terms, such as "allopatric forms" are deliberately used through much of this paper. The fine splitting on the species level affects classification on the higher levels. Most polytypic species or superspecies are treated by Mortensen as separate genera. Half of the 16 genera of echinoids represented in the West Indies by shallow water species consist of a single group of allopatric species or subspecies.

To make matters worse, different authors use different sets of taxonomic characters. A. H. Clark and H. L. Clark base their classifications primarily on the characters (spines and plates) of the dry tests, while Mortensen considers the structure of the pedicellariae as particularly sensitive indications of relationships. However, since these small and rather delicate organs are usually poorly or not at all preserved, the description is often based on a single specimen. Although this will

not invalidate the conclusions reached in this paper, there is a crying need for more, careful biometric studies of meristic and mensural characters.

A total of 16 genera (*Leodia* is here treated as a full genus) are known from the shallow waters of the West Indies (Clark, 1933); some species, of course, also extending into deeper waters. On the basis of distribution pattern and level of speciation, these 16 genera can be separated into four groups.

First Group

The first group consists of eight genera all of which are characterized by the fact that within each genus, all the known living species are allopatric:

Genus *Eucidaris* Pomel

This genus (Mortensen, *op cit.*, vol. 1 (text), pp. 384–411) illustrates geographic speciation almost diagrammatically (fig. 1). All 6 described forms are allopatric; and if all were considered as having the rank of subspecies only, the genus would become monotypic. Means of dispersal must be good in this genus, since some of the forms, particularly *metularia*, are very widespread. The genus, although consisting of essentially shallow water forms, was able to colonize St. Helena and Ascension, to cross the Atlantic from the West Indies to the Gulf of Guinea (or vice versa), and to spread through the Pacific from the coast of Africa to the Hawaiian Islands. Nevertheless, isolation has been sufficiently effective to permit considerable differentiation of the various isolates. The genus can be traced back to the Miocene in West Indian and North American deposits.

The degree of difference between the isolates is illustrated by the following differences between *tribuloides* (W. Indies) and *thouarsi* (E. Pacific): "the much broader median interambulacral space and smaller areoles of *tribuloides*, the larger size of the peristome in *thouarsi*, the existence of a limb on the stalk of the large globiferous pedicellariae in *thouarsi* but not in *tribuloides*, the much lighter color of the secondaries in *tribuloides*. . . ."

Genus *Astropyga* Gray

The three species of this genus are allopatric. (Mortensen, *op. cit.*, III_1, text, pp. 181–207). Best known is the widespread Indo-West Pacific species *radiata*, which extends from the East coast of Africa to Australia (Queensland) and Melanesia (New Britain); also known from Hawaii, but apparently not from any other island in Oceania. The other two species are: *pulvinata* (west coast of

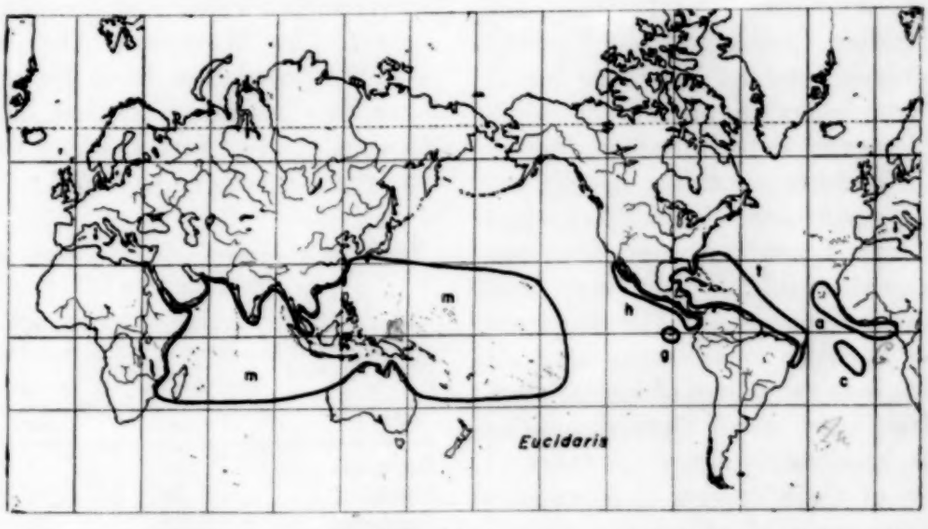

FIG. 1. Range of the species of *Eucidaris*. m = *metularia*, g = *galapagensis*, h = *thouarsii*, t = *tribuloides*, a = *africana*, c = *clavata*.

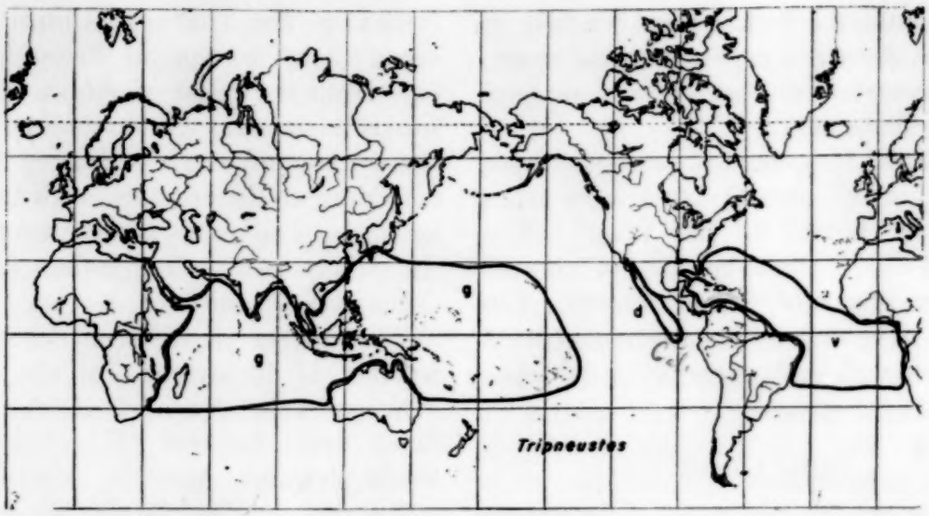

FIG. 2. Range of the species of *Tripneustes*. g = *gratilla*, d = *depressus*, v = *ventricosus*.

America from the Gulf of California to Panama) and *magnifica* (southern Florida, ? Jamaica). Origin of these species through geographic speciation is evident, although Mortensen considers the difference between *pulvinata* and *magnifica* too great to date back only to the late Pliocene closing of the Isthmus of Panama.

Genus *Tripneustes* L. Agassiz

The situation in the genus *Tripneustes* again is an almost diagrammatic demonstration of geographic speciation (fig. 2). (Mortensen, 1943, III_2, text, pp. 487–508). Three "species" are recognized by Mortensen: *ventricosus* (="*esculentus*") (Atlantic), *depressus* (E. Pacific), and *gratilla* (Indian Ocean and W. Pacific). The difference between the three forms, although unmistakable, are on the whole matters of degree, as for instance: Median areas of ambulacra aborally: usually not very bare (*ventricosus, depressus*)—usually very bare (*gratilla*); tubercles: usually very small (*gratilla*)—not very small (*ventricosus, depressus*). The diagnostic difference between *ventricosus* and *depressus* is given as: plates of buccal membrane: few, very small (*ventricosus*)—numerous, moderately large (*depressus*).

In spite of their narrow bathymetrical distribution, most of the forms have a very wide horizontal distribution, indicating considerable dispersal facilities. West African samples of *ventricosus*, for instance, are not clearly separable from West Indian samples. However, there is a certain amount of geographical variation within the range of each form. H. L. Clark (1933) states that the largest specimens he has seen come from the Bermudas. Jackson (1914) shows that the characters of the abactinal system indicate considerable geographical variation. In Jamaica, only 20 per cent of the adults reach the largest size class (diam. 110–132 mm.). In Bermuda, they measure much larger, reaching 145 mm. diam.

Contiguity existed no doubt formerly between *ventricosus* and *gratilla*, as stated correctly by Mortensen (*loc. cit.*). In fact, the population from Natal and Delagoa Bay appear somewhat intermediate between the two forms, which might indicate that once there has been a connection

Insertion of oculars in Tripneustes ventricosus *from Jackson (1914)*

Percentage of occurrence

	Oculars 1, 5 insert	Oculars 1, 2, 4, 5 insert	Other arrangements
Bermuda	61	2	37
Florida	46	12	42
Bahamas	22	27	51
Jamaica	19	40	41

around South Africa. In that case, the major break in this group would be between Hawaii and the Galapagos.

Ranking *ventricosus, depressus* and *gratilla* as subspecies of a single species (*gratilla*) would make the genus *Tripneustes* monotypic and would raise the question as to the valence of generic characters in this group of echinoids.

Genus *Mellita* Agassiz

The key-hole sea urchins consist of two groups of forms which are sometimes separated generically or subgenerically: *Mellita* (s. str.) for the forms with five perforations (lunules) of the test, *Leodia* with six (Mortensen, *op. cit.*, IV, 2, pp. 420–433). In the tabulation (table 2), they are treated as two genera.

Mellita. Three "varieties" are recognized by Mortensen in the five-holed species *quinquiesperforata.* These were originally described as full species (Clark, 1940, p. 435), but Mortensen cites convincing reasons why they should be considered only individual variants. *Mellita quinquiesperforata* occurs along the Atlantic coast of the Americas from Nantucket in the north to Brazil (Santos) in the south, and has been taken at Bermuda and in the Greater Antilles. Its representative along the Pacific coast of America is *longifissa,* distinguished by a very long posterior lunule, ranging from the Gulf of California to Ecuador. From the midst of the range of *longifissa,* Mortensen has described a "species" *M. grantii* based on a single specimen with a shorter posterior lunule and with shorter posterior petals. The status of this aberrant specimen can not be evaluated until more material is examined, and *M. grantii* is therefore ignored in the analysis.

Leodia. The distributional pattern of the six-holed species is virtually identical with that of the five-holed species. The Atlantic form *sexiesperforata* ranges from the Carolinas to the mouth of the La Plata, is found in Bermuda, and is widespread in the West Indies. The Pacific form *pacifica,* which differs by smaller radial lunules and the almost round, small, posterior lunule, is known only from Peru and Ecuador.

The species of the genus *Mellita* (except for the dubious *grantii*) illustrate geographic speciation perfectly. Dispersal powers in this group seem very limited since not a single form of the genus is found away from the Americas. Bermuda is the most isolated place the genus has been able to reach.

Genus *Moira* Agassiz

In his monograph, Mortensen (*op. cit.*, V_2, pp. 325–337) recognizes five allo-

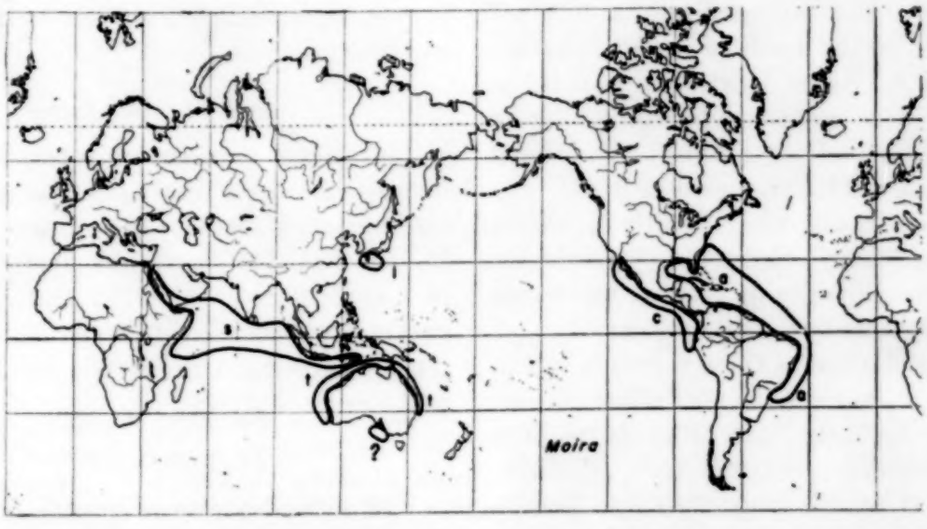

FIG. 3. Range of the species of *Moira.* s = *stygia,* t = *lethe,* l = *lachesinella,* c = *clotho,* a = *atropos.*

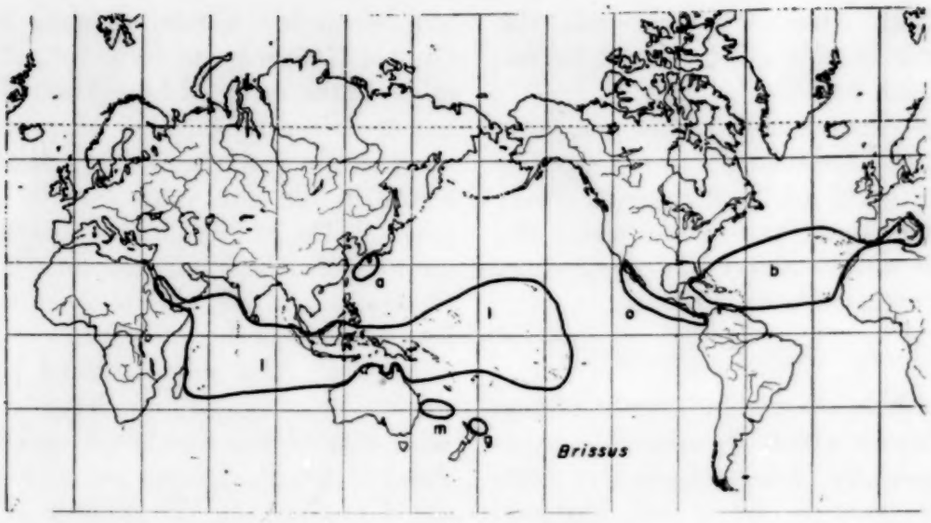

FIG. 4. Range of the species of *Brissus*. l = *latecarinatus*, m = *meridionalis*, g = *gigas*, a = *agassizi*, o = *obesus*, b = *brissus*.

patric species: *atropos* (Atlantic coast of Americas from N. Carolina to Santos, Brazil), *clotho* (Pacific coast, from Gulf of California to Ecuador), *lachesinella* (Japan), *lethe* (northern coast of Australia), and *stygia* (Zanzibar, Gulf of Suez, and Timor). It is doubtful that all of these deserve full specific rank. Regardless of the ultimate taxonomic arrangement, geographic speciation is evident (fig. 3).

Genus *Brissus* Gray

Six species of this genus are recognized by Mortensen (*op. cit.*, V_2, pp. 505–523). They are all apparently allopatric (fig. 4), but two of them (*agassizii* and *meridionalis*) differ in the teeth of the globiferous pedicellariae. Since Mortensen uses these teeth freely as generic characters, he is greatly disturbed at finding two forms which agree with their geographical representatives in all other details to differ in such a "basic" character. He finally resolves the difficulty by placing them into a separate subgenus (*Allobrissus*).

The distribution of these forms is as follows: (1) *brissus*, West-Indies (from Bermuda, Bahamas and Florida to Tobago), Adriatic and Western Mediterranean, and islands from the Cape Verdes to the Azores; (2) *obesus*, American west coast from the Gulf of California south to the Gulf of Panama; (3) *latecarinatus*, throughout the Pacific, from the Red Sea and Mauritius to the Hawaiian Islands, the Marquesas and Tuamotus; (4) *gigas*, no. New Zealand; (5) *meridionalis*, Norfolk Island and coast of New South Wales; (6) *agassizi*, so. Japan and Riukiu Islands.

Geographic speciation is evident, since all known forms are still allopatric. A noteworthy fact is that morphological deviation of almost generic rank occurs in peripheral populations in the cooler waters of the north (Japan) and south (Australia). It would be interesting if it could be demonstrated by further analysis of this group that "generic characters" vary geographically, as has been shown so often in birds.

Genus *Meoma* Gray

This genus contains only two allopatric forms, one east and one west of the Isthmus of Panama (Mortensen, *op. cit.*, V_2, pp. 524–531): *grandis*, from the Gulf of California to Colombia and the Galapagos, and *ventricosa*, West Indies, from the Mexican coast to Florida, the Bahamas and Lesser Antilles.

SECOND GROUP

The second group of genera consists of those in which there are cold water forms, in addition to the species of tropical wa-

ters. Actually, this group contains only a single genus, in which all warm water species are completely or essentially allopatric.

Genus *Lytechinus* A. Agassiz

In this genus, Mortensen (*op cit.*, III$_2$, text, pp. 434–462) recognizes 7 species. These are of unequal relationship to each other. Most distinct are the two Atlantic species *callipeplus* and *euerces*, which are furthermore not littoral species, but occur in cool waters between 100 m. and 500 m. Omitting these two isolated species, one is left with a more homogeneous group of forms. All of them are allopatric, except *pictus* and *anamesus* in the Gulf of California region. Mortensen thinks that these are good species, while H. L. Clark considers them only age stages (such as found in *Diadema*) or ecotypes (surf zone vs. quiet waters). Evidently, further work needs to be done before this problem can be considered as settled.

FIG. 5. Range of allopatric forms of *Lytechinus*. a = *anamesus*, s = *semituberculatus*, h = *panamensis*, c = *variegatus carolinus*, at = *var. atlanticus*, v = *var. variegatus*, p = *var. pallidus*, *L. callipeplus*, *L. euerces*, and *L. pictus* omitted.

The occurrence of geographic variation in this genus has long been recognized. The populations of *variegatus* from the Carolinas, Bermuda, the Cape Verdes, and the Caribbean are sufficiently distinct from each other to have been named either as separate species or as varieties. On the west coast of the Americas, the 3 "species" *anamesus* (California), *panamensis* (Panama) and *semituberculatus* (Galapagos and Ecuador) form likewise a group of close relatives that are at most on the borderline of subspecies and species status. Geographic speciation is, thus, very evident in this genus (fig. 5, in which the controversial "species" *pictus* is omitted).

Some authors place *Echinus verruculatus* (Lütken) in the genus *Lytechinus*, in spite of the differences pointed out by Mortensen (*op. cit.*, III$_2$, pp. 393–399). This Indo-Pacific species is strictly allopatric with *L. variegatus* but too old to be useful as a valid argument in favor of geographic speciation.

Third Group

The third group of genera illustrates the next step in the speciation process. When isolated allopatric populations have become sufficiently different genetically, they can invade each other's ranges and coexist as good species. In addition to having acquired reproductive isolation, they must also be sufficiently different ecologically so as not to compete too seriously with each other. This stage appears to be illustrated by 4 genera, although ecological information on two of them is lacking.

Genus *Echinometra* Gray

According to Mortensen (*op. cit.*, III$_3$, 1943, pp. 352–399), there are five species in this genus (fig. 6). They form three groups: (a) *lucunter* and *vanbrunti;* (b) *mathaei* and *insularis;* and (c) *viridis*. Except for *viridis*, all are so-called rock-borers. *E. mathaei* var. *oblonga* has been separated generically at one time, but with

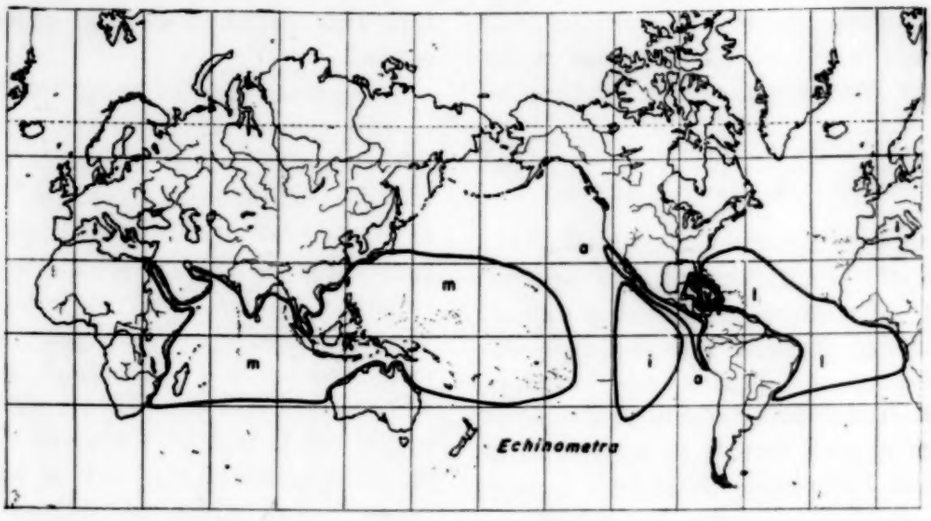

FIG. 6. Range of the species of *Echinometra*. m = *mathaei*, i = *insularis*, a = *vanbrunti*, l = *lucunter*, v = *viridis*.

little justification, as pointed out by Mortensen. Indeed, *insularis* is to such an extent intermediate between *mathaei* and *vanbrunti* that the relationship of these four species of "rock-borers" appears much closer than is usually admitted. All four are allopatric. They present a perfect picture of geographic speciation!

Of particular interest is the fifth species, *viridis*. Not only is it sympatric with *lucunter*, but it also has a very different ecology. It is not a "rock-borer," but lives on reefs under coral boulders. The geographical overlap between the two species was apparently made possible through the removal of competition owing to the change of ecology in *viridis*.

There is considerable geographical variation within *lucunter:* Specimens from Bermuda and Brazil (Abrolhos) are very large, African specimens are very dark, and specimens from St. Helena differ in several minor characters including the average number of pore pairs.

Genus *Diadema* Humphreys

In the genus *Diadema* (= *Centrechinus*), 6 species are recognized by Mortensen (*op. cit.*, III_1, text, pp. 241–281). Five of them are allopatric, and most of them are so similar to each other that there is no reason why they should not be considered subspecies. However, in the Indian Ocean and in the western Pacific, two very similar species coexist: *setosum* and *savignyi*. We evidently have here what in terrestrial island animals is called a "double invasion." Which of the two sympatric species was the earlier occupant of the area, and from where (east or west) the second invader came, still remains to be determined. The pattern of variation is exceedingly similar to that shown by *Eucidaris*, except for the overlap in the western Pacific (fig. 7).

D. savignyi is on the whole very similar to *setosum* but differs by having a blue pattern which is arranged in a ring on the apical system and in continuous lines down along the interambulacral midline. There is no reddish color around the anal opening, and the valves of the tridentate pedicellariae are straight, leaf or spoon shaped with serrate edges, not compressed. The interambulacra in the adult usually only with 5 series of large tubercles. The two species seem to live in separate colonies, but assumed hybrid specimens have been described. The blue color pattern is very susceptible to changes under the influence of light and darkness, and some of the reputed differences may not exist (Millott, 1953).

It is not evident from the handbook data how the double invasion of the western Pacific originated. *D. savignyi* has

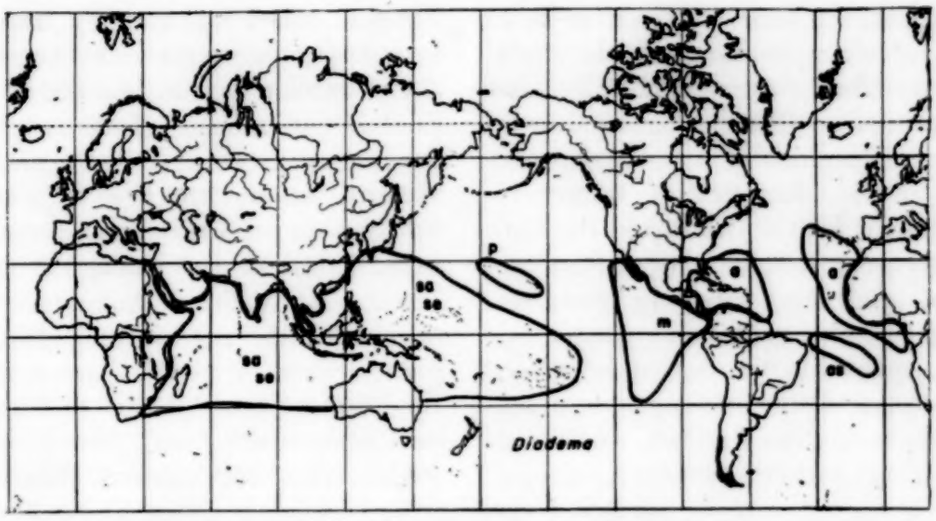

FIG. 7. Range of the species of *Diadema*. sa = *savignyi*, se = *setosum*, p = *paucispinum*, m = *mexicanum*, a = *antillarum*, as = *ascensionis*.

some characters of its own and some it shares with the other forms. The same is true for *setosum*. It will require a special taxonomic analysis to determine whether *setosum* or *savignyi* is more similar to *mexicanum* (trans-Pacific spread) or to *antillarum* (spread around the Cape of Good Hope). West African *antillarum* are curiously not different from Caribbean populations. In *setosum*, there is the possibility of a slight difference of the Japanese population (*"clarki"*) and of the Australian populations.

D. a. ascensionis is very similar to *antillarum*, differing mainly in the shape of the tridentate pedicellariae, and in details of the structure of the interambulacral tubercles and of the spines. The Hawaiian *paucispinum* is close to *mexicanum* and to *setosum*. Of *mexicanum*, Mortensen writes (p. 277): "This species is very closely related to *antillarum*, so closely indeed that were it not for the geographical reason of their areas of distribution being separated by the Isthmus of Panama, scarcely anybody would have thought of regarding them as two distinct species." Actually, of course, mere geographic isolation is no longer considered a species criterion.

Genus *Echinoneus* Leske

In this genus, Mortensen (*op. cit.*, IV, pp. 71–81) recognizes only two species. One is the almost cosmopolitan *cyclostomus* (West Indies from Bermuda to Tobago, Ascension, Pacific from the coast of Africa to Japan, the Hawaiian Islands, Easter Island and the east coast of Australia). The other is *abnormalis*, which is known only from Mauritius and some of the Indo-Pacific islands from the Moluccas to Hawaii. This species is in part sympatric with *cyclostomus*, but differs from it sufficiently so that some authors place it into a separate genus (*Koehleraster*).

Genus *Plagiobrissus* Pomel

Mortensen (*op. cit.*, V_2, pp. 494–504) recognizes five species which he assigns to two subgenera. In nominate *Plagiobrissus*, he places *grandis* (West Indies, from Florida and the Bahamas to Bahia, Brazil) and *africanus* (West Africa, Senegal to Gabun), which are so similar that it is difficult to state definite differences. Three other "species" are placed in the subgenus *Rhabdobrissus: jullieni* (Gulf of Guinea, West Africa), *costae* (Mediterranean, and eastern Atlantic, south to St. Helena), and *pacificus* (Gulf of California to Ecuador, Cocos Island).

In view of the overlap in the Gulf of Guinea, it is evident that at least two species or species groups are involved. The distribution is, however, peculiar. In particular, the isolated range of *pacificus* is

puzzling. H. L. Clark derived it from the West Indian *grandis,* which would seem reasonable zoogeographically, but Mortensen insists that the rounded frontal edge (distinguishing the two forms) is a taxonomic character of subgeneric rank! Except for the overlap in the Gulf of Guinea, there is strict geographical replacement of all the forms, and their origin by geographic speciation seems evident. It is probable that *jullieni* is derived from *costae,* and that *africanus* is a second invasion of the African west coast from the West Indies (*grandis*).

Fourth Group

The final group consists of those genera in which geographical overlaps have occurred so frequently and many species are so ancient, that the actual course, which speciation has taken, has become completely obscured. Such genera are usually rich in species. Three genera occurring in the West Indies belong to this group, *Arbacia* with 6, *Encope* with 9, and *Clypeaster* with 35 described species.

Genus *Arbacia* Gray

In this genus, Mortensen (*op. cit.,* II, text, pp. 562–580) recognizes 6 species. These are unequally distinct from each other. A pair of allopatric species, *punctulata* (American east coast) and *spatuligera* (American west coast), are obviously very close to each other, and perhaps best considered members of a single polytypic species. Likewise, another pair of allopatric species, *dufresnii* (southern South America) and *crassispina* (Tristan da Cunha, 180–270 m.), are sufficiently similar to each other to be treated in a similar manner. However, these two species (or species groups) are not particularly close either to each other or to the two remaining species of the genus. One of these is *stellata* (American west coast from Lower California to Peru; Galapagos Islands). The other is *lixula* with two subspecies: *lixula* (the Mediterranean and the Atlantic coasts of Africa south to Guinea; also Canaries, Madeira, and Azores; coast of Brazil) and *africana* (coast of Congo region and Angola). The complete distribution of some of the mentioned species is as follows: *punctulata* (Atlantic coast of North and Central America from Cape Cod to Florida, also north coast of Cuba and Yucatan; Curacao, Trinidad and Tobago); *spatuligera* (west coast of South America from Ecuador to Southern Chile); *dufresnii* (temperate coasts of South America from the La Plata on the Atlantic to Puerto Mont on the coast of Chile. Also Falckland Islands and some Antarctic Islands).

It is evident from these distributions that this genus has diversified to the extent that there are four actually or potentially sympatric species groups (*lixula, punctulata, stellata,* and *dufresnii*). In terms of geographic speciation, this means that the time of the speciation lies sufficiently far in the past for the original geographic relationships to have become obliterated.

Genus *Encope* L. Agassiz

The taxonomy of this genus is still far too confused to permit its use as material for speciation research. Of the species listed by Mortensen (*op. cit.,* IV_2, pp. 433–451) two are very distinct and not closely related to the others: *grandis* (Gulf of California) and *stokesii* (Pacific coast from Mexico to Ecuador, Galapagos Is.). The latter is now separated in the genus *Melitella* (Durham, 1950). The other "species" seem to form a closely knit group, although there is much doubt as to their relationship. On the Atlantic coast of the Americas only two so-called species occur, neither of which seems to extend to Bermuda, the Bahamas or Greater Antilles. It is probable that these two forms are actually sub-species of a single species, since *michelini* is restricted to the northern Gulf of Mexico (from Florida to Yucatan) while *emarginata* occurs to the north (Florida to South Carolina) and to the south (Brit. Honduras to the mouth of the La Plata).

On the Pacific coast, the situation ap-

pears much more complicated. Three species (in addition to *E. grandis*) are reported to live sympatrically in the Gulf of California: *E. californica* (L. California), *E. perspectiva* (L. California) and *E. micropora*. Any of these might be the west coast representative of *E. emarginata*. There are the additional species *E. wetmorei* (Panama) and *laevis* (Nicaragua) which may or may not be local subspecies of *micropora*.

Most of the living species are represented by fossils from Pleistocene and Pliocene, and some as far back as the Miocene (Durham, 1950). The rather active speciation of *Encope* appears to be due to limited dispersal facility in this genus which leads to an apparent localization of populations and gives natural distributional barriers greater efficiency. It would be interesting to know more about the larval biology of this genus. Like *Mellita, Encope* has been unable to spread beyond the Americas.

Genus *Clypeaster* Lamarck

The taxonomy of this genus is still very confusing. Mortensen (*op. cit.*, IV_2, text, pp. 5–132) lists no less than 35 binomials in 10 sections (= subgenera). The definition of these sections appears in part to be highly artificial and arbitrary. As a result, the West Indian *rosaceus* is placed in the same section with *pallidus* from Hawaii and with *eurypetalus* known from a single specimen from the central Pacific. Surely *rosaceus* should have a representative along the west coasts of the Americas as well as in the Indian Ocean. There is a suspicion that a better knowledge of the genus would lead to a very different classification. Geographical representatives of *rosaceus* occur presumably in several sections. *Clypeaster rosaceus* is exceedingly common in the West Indies, and it is therefore puzzling that it has been found so rarely along the coasts of Central and South America. Mortensen does not record it from there, but there is a specimen from Belize (Brit. Honduras) in the U. S. National Museum.

A second West Indian species, *C. subdepressus*, is especially characteristic of muddy bottoms. Its distribution in the Caribbean is therefore irregular. What its nearest relatives are is obscure.

Geographic speciation

Geographic speciation proceeds in two steps. During the first, a species breaks up into geographical isolates which diverge from each other genetically. The second step consists of the secondary overlap of some of these populations, without interbreeding. Both steps are abundantly illustrated among the shallow water, tropical sea-urchins. As table 1 shows, more than 75 per cent of all forms within a genus are allopatric, and half of the genera consist entirely of allopatric forms. It is immaterial in this consideration whether all the allopatric forms listed as species by Mortensen are really species. It is evident that every stage is represented among these isolates from slightly differentiated populations and distinct subspecies to full

TABLE 1. *West Indian shallow water echinoids*

Name of genus	Number of allopatric forms	Number of additional sympatric species
Eucidaris	6	—
Diadema	5	1
Arbacia	3	3
Lytechinus	4	?1 (+2)[1]
Astropyga	3	—
Tripneustes	3	—
Echinometra	4	1
Clypeaster	(?)[2]	(several)[2]
Mellita (Mellita)	2	?1[3]
Mellita (Leodia)	2	—
Encope	4 (+?2)[2]	3 (+?2)[2]
Echinoneus	1	1
Moira	5	—
Plagiobrissus	4	1
Brissus	5	—
Meoma	2	—
Total[4]	53 (+?2)	12 (+?4)

[1] Deep water species.
[2] Taxonomy of this genus still obscure.
[3] The status of *grantii*, based on a unique specimen, is yet to be determined.
[4] Omitting *Clypeaster*.

species. This is precisely as is demanded by the theory of geographic speciation.

If one of these isolates, after having acquired reproductive isolation and ecological compatibility, invades the range of one of its sister species, the two can coexist side by side. Various cases of sympatric species are known among these genera. In *Diadema*, the two species *setosum* and *savignyi* coexist in the western Indo-Pacific. We have here presumably a case of "double invasions," which are so well known among terrestrial insular animals. However, the taxonomy of this genus is not sufficiently matured to permit us to determine the exact derivation of the two species. The genus *Lytechinus* likewise offers cases of sympatric species. Leaving aside the dubious form *pictus*, there are the two Atlantic species *callipeplus* and *euerces* which occur in the same geographical area as the littoral *variegatus*. However, *callipeplus* and *euerces* live in a different ecological zone, being found between 100 m. and 500 m. They are rather old species whose origin is uncertain. It is possible that *callipeplus* was originally a West African species which only secondarily invaded the West Indian range of *euerces*. The overlap of *Echinometra viridis* with *E. lucunter* was discussed above. It is most interesting that this sympatric species is the only *Echinometra* which is not a "rock-borer." Sympatry was apparently made possible only by this shift of ecological niche. In the genus *Clypeaster*, a number of sympatric species occur but their taxonomy is too confused to make any further discussion meaningful; the same is true for the genus *Encope*. In *Echinoneus*, there is *abnormalis* of the Western Indo-Pacific which is sympatric with the cosmopolitan *cyclostomus*. The separation is obviously old, since *abnormalis* is often generically separated (*Koehleraster*), and the history of the speciation is obscure. Finally, in *Plagiobrissus*, there is overlap in Western Africa between at least two species. Here, the history of this overlap could perhaps be reconstructed if the relationship of *grandis*, *costae*, *jullieni*, and *africanus* was better understood.

The important point is that sympatric species are generally quite different, much more different than the allopatric "species," so that it must be assumed that their origin lies in the more distant past. Although not proving geographic speciation, such distribution is consistent with it.

The sympatric occurrence of sibling species, such as that of *Diadema setosum* and of *D. savignyi*, is nothing exceptional; and similar cases have been found, for instance, in the genera *Strongylocentrotus*, *Encope*, *Echinothrix*, *Parasalenia*, *Echinostrephus*, and *Heterocentrotus*. The only reason why such cases are here mentioned is because they have been cited as evidence against geographic speciation. This argumentation overlooks various important points. One is that the amount of genetic difference between sibling species is of the same order of magnitude as that between morphologically more distinct species. There is no reason to postulate for sibling species a different speciation mechanism than for morphologically more distinct species. A second reason is that sibling species occur commonly also in groups in which the universal occurrence of geographic speciation is acknowledged, as in birds, mammals, and butterflies.

Age of species. Several genera of echinoids are quite well represented by fossil specimens, and it should be possible to utilize this information to determine rates of speciation (Grant and Hertlein, 1938). Incomplete taxonomic analysis, however, makes this impossible at the present time. Eleven described species of *Encope* are, for instance, known as fossils from the Gulf of California area, where now only 4 (+ 1) Recent species occur (Durham, 1950). The fossil species are often clearly portions of lines leading to recent species: *chaneyi* (Lower Pliocene)—*shepherdi* (Upper Pliocene)—*inezana* (Pleistocene)—*grandis* (Recent); *carmenensis* (Upper Pliocene)—*arcensis* (Pleistocene)—*micropora* (Recent). However, one of the fossil species,

sverdrupi (Lower Pliocene), seems to have no Recent counterpart, and one of the Recent species (*perspectiva*) no fossil counterpart. Finally, *californica* seems to be represented in lower Pliocene by *tenuis, loretoensis,* and by *californica* (indistinguishable from Recent), and *grandis*-like specimens have been found in the Miocene of Florida. This fossil difficulty cannot be resolved until the true relation of the Recent species *emarginata, micropora, perspectiva, californica, laevis* and *wetmorei* has been fully elucidated. The available evidence indicates that most of the lines have existed since the lower Pliocene (12 million years ago), although usually considered specifically distinct from their Recent descendants, and that since that period, one line may have become extinct and another invaded the area.

Even Miocene species are not strikingly different from their Recent descendants, and a period of 20–25 million years might be in many cases a more precise estimate of the length of time required for the development of a new species. This is particularly evident when we consider that genus and polytypic species often coincide in echinoids and that many of the genera of echinoids may go back to the Eocene (40–60 million years ago).

Dispersal barriers

Geographic speciation depends on geographic isolation by extrinsic barriers. What is the nature of the barriers which separate populations of sea urchins? As is well known, barriers are relative, their efficiency depending on the dispersal facilities of the organism which they confine. Hence the importance of the study of dispersal. Apparently all of the studied sea urchins achieve dispersal through free-swimming pelagic larvae. Since some species have very wide ranges, others narrow ones, one might assume that there are differences between species in length of larval priod or tolerance to adverse water conditions, but no such information is as yet available. Typical distribution patterns of widespread species are:

Western Indo-Pacific (often from Africa to Hawaii)—*Eucidaris metularia, Diadema setosum, D. savignyi, Tripneustes gratilla, Echinometra mathaei, Echinoneus abnormalis,* and *Brissus latecarinatus.*

Caribbean and coast of West Africa (either identical or only slight subspecific differences)—*Eucidaris tribuloides, Diadema antillarum, Lytechinus variegatus* (with *pallidus*), *Tripneustes ventricosus,* and *Echinometra lucunter.*

Outlying oceanic islands, such as the Galapagos, St. Helena, Ascension, Easter Island, Marquesas and Hawaii, are frequently colonized by these shallow water forms, undoubtedly by planktonic colonization.

On the other hand, the species in some other genera are amazingly confined: *Lytechinus* is absent from Africa (except Cape Verde Islands) and *Plagiobrissus* from the western Indo-Pacific; *Mellita* (*Mellita*), *Mellita* (*Leodia*), *Encope,* and *Meoma* are restricted to the Americas.

Of the existing barriers, by far the most potent has been that between Polynesia and the American west coast, as pointed out by Ekman (1935, 1946). Presumably the distance is too great even for pelagic larvae to cross the gap easily. Furthermore, there are various ecological reasons (direction and temperature of currents) to discourage such dispersal. See also Gislèn (1944) for a slightly different evaluation of the situation.

The Central American barrier. The gap between the Pacific and the Caribbean across the Isthmus of Panama was closed in the Upper Pliocene about 2,000,000 years ago. This event permits a fairly precise dating of the time of origin of the differences between populations, subspecies and species east and west of this new barrier. There are several tabulations in the literature of species in fishes, crabs, pycnogonids, and molluscs which seem to have originated since that event. As far as the shallow water sea urchins are concerned, it is interesting that not a single species is identical on both sides of the Isthmus (table 2). Unfortunately, echi-

TABLE 2. *Speciation on both sides of the Isthmus of Panama*

	Caribbean	E. Pacific
Eucidaris	*tribuloides*	*thouarsii*
Arbacia	*punctulata*	*spatuligera*
Astropyga	*magnifica*	*pulvinata*
Diadema	*antillarum*	*mexicanum*
Lytechinus	*variegatus*	*panamensis*
Tripneustes	*ventricosus*	*depressus*
Echinometra	*lucunter*	*vanbrunti*
Mellita (Mellita)	*quinquiesperforata*	*longifissa*
Mellita (Leodia)	*sexiesperforata*	*pacifica*
Encope	*emarginata*	*micropora*
Moira	*atropos*	*clotho*
Plagiobrissus	*grandis*	*pacificus*
Brissus	*brissus*	*obesus*
Meoma	*ventricosa*	*grandis*
Clypeaster	*rosaceus*	—
Echinoneus	*cyclostomus*	—

noid taxonomy has not yet advanced to the point where it could be stated whether these differences are of subspecific or specific significance. It appears probable that most of the differences are only subspecific. Additional cases among the starfishes and ophiuroids are cited by Ekman (1946) who gives a thorough discussion of this problem, as he has also done in his earlier book (1935, pp. 48–58).

A representative "species" occurs on the American west coast in 14 of the 16 genera from the Caribbean (table 2). In most cases, colonization seems to have taken place from the Caribbean to the Pacific. However, the tenuous hold which some of these forms have on the American west coast is likely more to reflect adverse ecological conditions (Gislèn, 1944) than recent arival. Mortensen and Gislèn call attention to the great age of many echinoid species and are therefore not convinced that all the differentiation, reflected in table 2, has occurred after the closing of the Panama gap. This is, for instance, insisted upon by Mortensen (*op. cit.*, III_1, pp. 181–207) for the species *Astropyga magnifica* (Caribbean) and *A. pulvinata* (W. America). It requires a more penetrating analysis before these species pairs can be separated into old and recent ones.

Southwestern Africa with its cold waters is a fairly effective barrier between warm water forms of the Atlantic and Indian Oceans, although the similarity of some of the west and east African elements and other evidence indicates that occasional faunal exchange around the Cape of Good Hope must have been possible.

Some of the genera are peculiarly unable to jump certain gaps, such as *Arbacia* and *Encope* from the American mainland to the Bahamas, across the 60 miles of Gulf Stream. No doubt a study of larval dispersal might shed light on these puzzling distributional problems. There is some evidence that the reduced dispersal facility of *Encope* is correlated with an increased amount of speciation. At the same time, some of these irregularities of distribution are due to specialized habitat requirements which cannot be satisfied in certain areas. Such unsuitable habitats are as much distribution barriers as adverse currents or land barriers.

All the treated species of echinoids seem to have a rather long pelagic larval period, to judge from the scanty literature. Presumably, this leads to a considerable dispersal and results in a thorough mixing of populations. This would explain the wide ranges of most of the forms. The conclusions arrived at in this paper are therefore valid only for forms with easy dispersal. In groups that lack a stage with free-swimming pelagic larvae, there will be presumably more geographical barriers; the ranges of the species may be smaller, and perhaps speciation more active. A thorough analysis of such groups would seem very important.

Slight geographic variation

The pronounced differences between geographic isolates, usually listed as full species in the echinoid literature, are foreshadowed by local variation even within these "species." Such variation is, of course, evident only where whole series of specimens from different localities are studied. The outstanding work on this problem as it relates to echinoids was done

by Jackson, particularly in his Studies of Jamaica Echinoids (1914). It is one of the few studies in echinoderms, known to me, in which large population samples were analyzed (for instance, 1400 specimens of *Diadema antillarum*). The variation of *Lytechinus variegatus* involves color, the size of the spines, the arrangement of the plates (table, p. 9) and other characters.

A particularly thorough study of slight geographical variation is that of Vasseur (1952) on *Strongylocentrotus droebachiensis* and *S. pallidus*. Such slight geographic variation occurs in many marine invertebrates and has been described especially in the starfishes (Döderlein, 1917, 1920; Engel, 1934; Tortonese, 1949, 1950, and others). That the asteroids show clear evidence for geographic speciation has been specially emphasized by Tortonese (1950) who quotes examples in the genera *Echinaster, Astropecten, Protoreaster, Oreaster, Porania, Asterina, Psilaster, Benthopecten, Asterias,* and *Hippasteria*. Many of these genera contain evident polytypic species; in other cases, the allopatric forms are on the borderline between subspecies and species, or else they are too different to be considered anything but good species. Thus we have here again numerous cases of an almost diagrammatic demonstration of geographic speciation. Many cases of minor geographic variation and of character gradients are described by Fisher (1911–1930).

In addition to geographic races, there occur among marine animals phenotypically different populations which are characterized ecologically rather than geographically (Tortonese, 1950). However, if these cases are studied in detail it is found that such populations completely grade into each other. In shallow water populations of the starfish *Astropecten irregularis* Pennant, for instance, there is a tendency toward an increased formation of spines (var. *irregularis*, var. *serratus*) (Engel, 1934). In littoral echinoids likewise, it is sometimes found that individuals dredged from greater depths are slightly different from the shallow water forms. This variation with depth is a response to local environmental conditions and is as gradual as is "altitudinal variation," the corresponding phenomenon in land animals. Such ecotypic adaption of populations to local conditions does not isolate these populations from each other and does not lead to speciation.

The Occurrence of Polytypic Species Among Marine Animals

The situation described above for echinoderms and more especially for echinoids is not unique among marine animals. Rensch (1947) refers to recent literature on polytypic species in tunicates (Eisentraut), echinoderms (Engel, Heding), cephalopods (Adam), cumaceans (Zimmer), anthozoans (Pax, Jaworski, Frenzel), and sponges (Arndt).

This includes species of very different ecology. It supports the assumption that geographic speciation is, among marine animals, not restricted to shallow water tropical species (such as the West Indian echinoids). Although no recent monographs as thorough and reliable as Mortensen's are available, a cursory examination of the literature of deep sea and pelagic groups indicates that in them speciation is just as much geographic as in the echinoids. The living crinoids are largely deep sea bottom forms. In the crinoid family Thalassometridae, Clark (1950) lists 61 species. Of these, 6 are poorly known (species inquirendae) and may be synonyms. These may be eleminated from further discussion. Among the remaining 55 species, 29 appear to be "good" species, while the other 26 species (= 47 per cent) are allopatric to these 29 species and so similar to them that intergradation might well be proven in many cases if more material were available. Most of these 26 "species" might well have to be considered subspecies. In the closely related family Charitometridae, the results are very similar. Of 32 species, 3 are species inquirendae. Among the remaining, 20 are good species, and 9 (= 31 per

cent) are potentially subspecies. These data suggest the frequency of geographic speciation among deep sea forms.

A similar picture is suggested by the pelagic jellyfish (Scyphomedusae). Their taxonomy is still very poorly understood, and the following extracts from Mayer's monograph (1910) are cited merely to indicate the possibilities in this group. They suggest, however, that most of the genera contain (or are entirely composed of) polytypic species and superspecies. No effort was made to bring the nomenclature up-to-date or to analyze the literature since Mayer.

Pelagia (p. 570)

noctiluca (Mediterranean and eastern tropical Atlantic)
cyanella (West Indies to Gulf Stream)
flaveola (Tropical Pacific, from East Africa to South America)

Chrysaora (p. 577)

hysoscella (Mediterranean and eastern Atlantic)
blossevillei (Atlantic coast of South America)
plocamia (Pacific coast of South America)
helvola (North Pacific)
calliparea (coast of east Africa and Indian Ocean)

Dactylometra (p. 583)

lactea (western South Atlantic, Brazil to West Indies)
quinquecirrha (western North Atlantic, Florida to New England)
africana (coast of Southwest Africa)
ferruginaster (Pacific coast of Japan)

Cyanea (p. 595)

capillata (North Sea to Norway)
arctica (American coast north of Cape Cod)
fulva (Cape Cod to Carolina)
versicolor (Carolina to Florida)
ferruginea or *postelsii* (North Pacific)
nozakii (inland sea of Japan)
annaskala (temperate coast of Australia)

Discomedusa (p. 606)

lobata (Mediterranean)
undulata (Gulf of Guinea)
philippina (Philippines)

Phacellophora (p. 612)

ambigua (Pacific coast of North America)
sicula (Japan, Mediterranean)
ornata (Atlantic coast of North and South America)

Aurelia aurita (p. 619)

aurita (Mediterranean, coast of Europe)
colpota (Indian Ocean and tropical Pacific)
flavidula (Atlantic coast of North America)
hyalina (North Pacific)
dubia (Persian Gulf)

Cassiopea andromeda (p. 637)

polypoides (Red Sea)
andromeda (Indian Ocean and Malay Archipelago)
acycloblia (Moluccas)

Cassiopea ornata (p. 648)

ornata (New Guinea, Micronesia)
digitata (Malay Archipelago)
depressa (Indian Ocean)
picta (Red Sea)

The ranges of these pelagic forms are usually different from those of the littoral echinoids, and so are the geographical barriers. Also, as the work of Pickford (1946) and Haffner (1952) has shown, the ranges of pelagic forms are essentially three-dimensional. Nevertheless, these data, crude as they are, give a good indication of the frequency of polytypic species and super-species in pelagic coelenterates.

Conclusion

The data presented in this paper, particularly on echinoderms, can be interpreted as indicating that geographic variation is extremely widespread among marine animals. The range of the nearest relative of a given species is usually allopatric. Marine animals agree in this pattern of variation and distribution completely with terrestrial animals in which geographic speciation has been demonstrated. This fact suggests that geographic speciation is the principal, if not exclusive, speciation mechanism in most marine animals.

The studied marine forms reproduce sexually, and either live pelagically (scyphomedusae) or have at least a pelagic larval stage (most echinoids). The fact that speciation in such forms is normally geographical does not rule out the possibility of the occurrence of other processes of speciation in marine organisms with a

different ecology or a different reproductive pattern. The groups, in particular, in which temporary or permanent asexual reproduction occurs require further study.

Summary

If the world distribution of the 16 genera of West Indian shallow water echinoids is mapped, it is found that each genus consists of one or several groups of allopatric species (see maps). The differences between many of these allopatric "species" is sufficiently slight to indicate that some are better considered subspecies

Allopatric populations show every grade of distinctness, ranging from mere statistical difference through subspecific to specific rank. Superspecies are frequent. This pattern of geographic variation is the same as that found in terrestrial animals with geographic speciation.

Geographic speciation is also suggested by the distribution pattern of groups with a different ecology, such as deep sea organisms (crinoids) and pelagic organisms (scyphomedusae).

The eastern Pacific, the Isthmus of Panama and the cold waters of southwest Africa appear to be the most important dispersal barriers and hence speciation agents for warm water echinoids.

The presented data indicate that the prevailing speciation process in sexually reproducing marine animals is that of geographic speciation. No evidence was found which would require any other mode of speciation.

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TRENDS IN GEOGRAPHICAL VARIATION IN PALAEARCTIC MEMBERS OF THE GENUS PARUS

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INTRODUCTION

The writer has recently completed a survey of the Palaearctic members of the genus *Parus*, which it is hoped will be published in full elsewhere. In the course of the work the importance of the so-called "ecological rules" (Bergmann's, Allen's, Gloger's and a rule for tail-length) became apparent, accounting straight away for most of the observed geographical variation of species with continuous ranges and some of that observed in species with discontinuous ranges. Bergmann's rule was, however, found to need some modification, and some amplification of all the rules was necessary when comparisons were made between species. The purpose of this paper is to give an account of these climatic trends in variation, and to discuss briefly their bearing on questions of adaptation. Since a fuller account is being prepared, the treatment here will be condensed. But it is hoped that the attention of systematists may be directed to the possibility of finding similar modifications and amplifications of the ecological rules in other groups.

The genus *Parus*, comprising the tits and chickadees of the Old and New Worlds, contains 30–40 species of small, agile, hole-nesting birds with short beaks, which exploit the branches, twigs and leaves of trees for feeding. Many of them have very wide geographical ranges, and in many areas several species occur together, often as many as four or five in the same habitat. Their colours are varied but mostly subdued, the upper parts being of various shades of grey, blue-grey, brown, olive or green, the under parts usually pale, with some buff or yellow, and the head often with some pattern of black or white. They have long been a favourite genus for bird systematists, and the ecology and behaviour of some species have been thoroughly investigated (e.g. Odum, 1941/2; Dixon, 1949; Gibb, 1950; Kluijver, 1951; Hinde, 1952).

The Eurasian members of the genus fall rather naturally into several groups, which may be conveniently listed here:

Major group.	*P. major, p. monticola, P. nuchalis.*	Whole of Eurasia.
Cyanistes group.	*P. caeruleus, P. cyanus.*	Western Palaearctic, northern and central Asia.
Periparus group.	*P. ater, P. melanolophus, P. rubidiventris.*	Whole Palaearctic Region.
Lophophanes group.	*P. cristatus, P. dichrous.*	Europe and Himalayas.
Poecile group.	*P. palustris, P. atricapillus, P. lugubris, P. cinctus, P. davidi, P. superciliosus.*	Whole Palaearctic Region.
Sittiparus group.	*P. varius, P. semilarvatus.*	Japan, Korea and Philippines.
Pardaliparus group.	*P. elegans, P. venustulus, P. amabilis.*	Central and southern China, Philippines.
Machlolophus group.	*P. xanthogenys, P. holsti.*	India, southeastern Asia and Formosa.

The first five groups only have been studied in detail. The ranges of the others lie mainly outside the Palaearctic Region, except for the the distinct *Sittiparus* group, which shows morphological convergence to the nuthatches (*Sitta*) and has been omitted for lack of any information on its ecology. Eight species, *P. major, P. caeruleus, P. cyanus, P. ater, P. cristatus, P. palustris, P. atricapillus* and *P. cinctus,* have very wide ranges within the Palaearctic Region and are well represented in museums. It is these species that afford most of the detailed data on which the conclusions in this paper are based.

Outside Eurasia, several species of the genus occur in the Ethiopian Region (*Melaniparus* group), and several in North and Central America (*Poecile* and *Baeolophus* groups).

Geographical Variation in Size

In all the species for which enough data exist to be able to test the point, wing-length is negatively correlated with the winter temperature, as indicated by the mean temperature of the coldest month. No correlation has been found between wing-length and the mean temperature of the warmest month (cf. Rensch, 1939). There is some correlation with the annual range of temperature, but this is merely because the areas with the coldest winters, being continental, tend to have the greatest annual range. Further, in all except one of the species for which weights are available, wing-length has found to be a satisfactory indication of general size. (The partial exception is *P. major,* in which British weights are unexpectedly high.) There is little doubt, therefore, that an increase in size with decreasing winter temperature (Bergmann's rule) is general in the genus.

The relationship between wing-length and the mean temperature of the coldest month differs in different species. In *P. major* (fig. 1) and *P. caeruleus,* for which the most complete data are available, it is found that as temperature decreases wing-length at first increases sharply over the higher ranges of temperature, and thereafter, at lower temperatures, more slowly. In addition, in these and other widespread species there are two main complicating factors.

(1) With the same winter tempera-

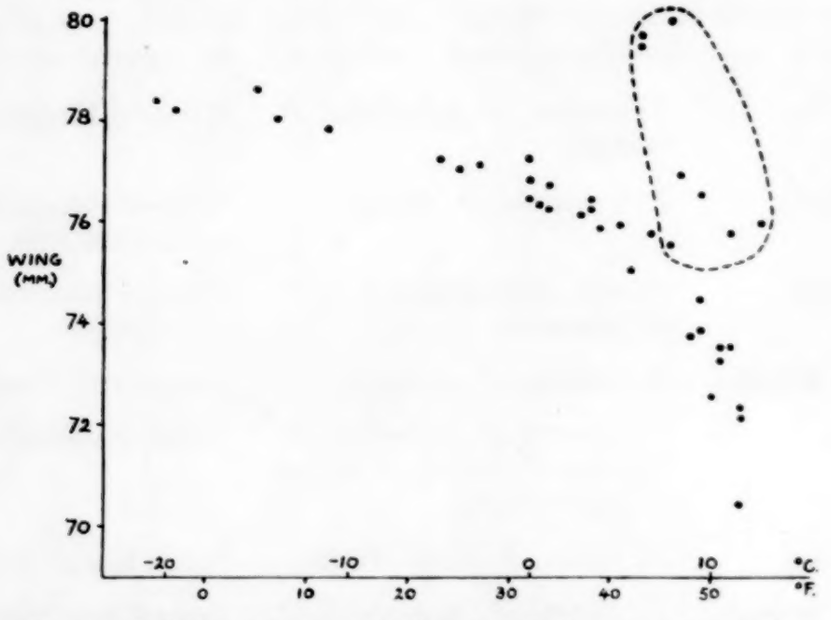

Fig. 1. Relation between wing-length and the mean temperature of the coldest month in 39 populations of *P. major, major* section. The North African populations and one from southern Persia are enclosed by the broken line.

tures, wing-length tends to be greater at lower latitudes than it is at higher latitudes. This "latitude effect," as it may be called, produces more marked differences in some species than in others. It is especially striking when populations of *P. major, P. ater, P. cristatus* and *P. palustris* from the mountains of southern Europe or northwest Africa are compared with more northerly lowland populations: the former are larger, in some cases much larger, in spite of higher winter temperatures. As a result of this combination of Bergmann's rule and latitude effect, in widespread species of *Parus* the largest birds are generally found not in the north, but in mountainous regions in the south of the range. In some species in which the latitude effect is well marked (e. g. *P. ater* and *P. cristatus* (fig. 2)), it may swamp the effect of Bergmann's rule, unless comparisons are made only between populations from approximately the same latitude.

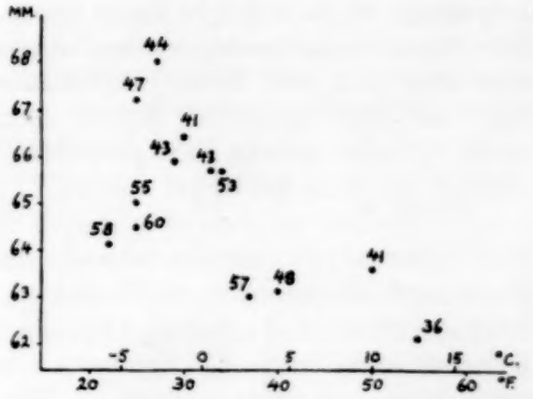

FIG. 2. Relation between wing-length and the mean temperature of the coldest month in 13 populations of *P. cristatus*, with the latitude of each locality.

The latitude effect has been found in all the species in which the north-south range is extensive enough to test it; hence some general environmental relationship is evidently involved. Possibly, it is rather that at high latitudes some factor inhibits the operation of Bergmann's rule than that its operation is enhanced at low latitudes. The accepted adaptive basis of Bergmann's rule is that of heat-conservation. For this purpose it should be advantageous for birds to be of the same size, for equivalent winter temperatures, in the north as in the south. But although the amount of food required will be relatively less, size for size, for a larger than for a smaller bird, the absolute amount needed per day must, other things being equal, be greater for the larger bird. It may be, therefore, that in the north, where the winter days are very short (5–5½ hours' feeding activity in Lapland in January, at least 9 hours' in North Africa), selection will act against the attainment of the size most efficient for heat-conservation.

On this explanation, the importance of the latitude effect for any species would be expected to depend at least partly on its feeding ecology. The five species in which it can best be judged can be put into the following order:

P. major *P. caeruleus*	Latitude effect not marked, except in the extreme south of the range (fig. 1).
P. atricapillus	Latitude effect more marked.
P. cristatus *P. ater*	Latitude effect so marked as to obscure the relationship of wing-length to temperature (fig. 2).

These are in fact in order of decreasing size and increasing fineness of beak. It seems possible that the limitations imposed on food-finding by a very short winter day would be most important for small species with fine beaks, because they would tend to take smaller food particles, i.e. they would feed less efficiently per unit of time, than larger species. Observations on the British species support this hypothesis. Gibb (unpublished) has shown that even in England in winter the

percentage of the daylight hours spent by *Parus* species in feeding varies inversely with their size, and Betts (unpublished) has found that the smaller British species do in fact tend to take food particles of a smaller size than the larger species.

(2) Different sections of a species may show different relationships between wing-length and temperature, as illustrated by three sections of *P. major* (fig. 3: see Delacour and Vaurie (1950) for a systematic review of these sections). This is not surprising. Long-isolated sections of a species will be expected to have evolved physiological and ecological differences, which will tend to alter their adaptive response to the environmental temperature. They may also have evolved morphological differences, which will alter the relationship between wing-length and body-size.

In figure 3 it is interesting to compare the curves for the three sections. For equivalent winter temperatures the *minor* section is considerably smaller than the *major* section: in the Amur Valley, where they meet without interbreeding (Stegmann 1931), the curves for these two sections are well separated, the difference in mean wing-length being over 4 mm. It is easy to suppose that hybrids produced in this region would be poorly adapted to their climatic environment. On the other hand, the *major* and *cinereus* sections, for which the curves are very similar, hybridise in Persia (Vaurie, 1950), and the *minor* section hybridises with the *cinereus* section in the warmest part of its range (central and southern China), where its size/temperature curve meets that of the *cinereus* section.

FIG. 3. Relation between wing-length and the mean temperature of the coldest month in the *major, minor* and *cinereus* sections of *P. major*, schematically shown. Solid lines: *major* section (Europe, southwestern Asia and Siberia), as in figure 1. Broken lines: *minor* section (China and Japan). Dotted lines: *cinereus* section (India and southeastern Asia). A: Amur Valley populations of *major* and *minor* sections. (The fourth section of the species, the *bokharensis* section (central Asia), has been omitted through lack of adequate data.)

Since size must be closely related to feeding ecology, there must always be an interaction between adaptation to environmental temperature and ecological demands. It is to be expected on theoretical grounds that when sections of a species are isolated in regions with different climates while remaining in approximately the same ecological niche, their size/temperature relationships will be modified in such a way that the size adapted to the ecological niche is maintained in each section. That such a process does in fact occur is suggested by the isolated eastern and western Palaearctic sections of *P. palustris,* which meet with very different winter temperatures at similar latitudes.

Within the European range of *P. palustris,* mean January temperatures vary from about 39° to 25° F., and the mean wing-lengths of different populations from 63.0 to 67.0 mm. Within the eastern Palaearctic range of the species, mean January temperatures vary from about 25° to − 10° F., and the mean wing-lengths from 61.3 to 68.5 mm. Thus although one lives in a very much colder region than the other, the mean wing-lengths of populations of both sections are grouped about a middle value of 65 mm., though the size-range is, like the temperature-range, greater in the eastern section.

When different species are compared, the climatic rule of size variation breaks down entirely. For instance, the tits of of Lapland are not obviously larger than

TABLE 1. *Relative tail-length (expressed as a percentage of wing-length) in three members of the* Poecile *group.* To show the tendency for the more northerly species to have longer tails than the more southerly, and for relative tail-length to increase in the colder parts of the range.

P. cinctus	—		Scandinavia	96	E. Siberia	100
P. atricapillus	Holland	85	Scandinavia	91	E. Siberia	96
P. palustris	Pyrenees	82	Scandinavia	86	E. Siberia	97

those of India, and in the *Poecile* group (a well-defined section of the genus comprising the chickadees and allied species) the largest species of all, *P. lugubris,* is the most southerly. Obviously at this higher systematic level the different ecological demands are of paramount importance, so that climatic trends are likely to have been obscured by other adaptations.

GEOGRAPHICAL VARIATION IN RELATIVE TAIL-LENGTH

Well-marked differences in relative tail-length have been found in different populations of *P. major, P. caeruleus, P. ater, P. cristatus, P. palustris, P. atricapillus* and *P. cinctus.* In the first two species these variations show no simple correlation with any environmental factor, being most marked in the most isolated populations, but in all the others the tail is relatively longer in the colder parts of the range, increasing clinally from west to east across northern Europe and Siberia, where the range permits it; and such variations as have been detected in *P. nuchalis, P. melanolophus* and *P. dichrous* also point to a greater relative tail-length in the colder parts of their ranges.

When species are compared, the same trends appear. The more northerly species tend to have longer tails than the more southerly, or, where the latitudinal range is the same, those living in the colder area tend to have longer tails than those in the warmer area. This is particularly well illustrated in the *Poecile* group of species. The three species whose distribution extends from west to east across northern Asia occupy different latitudinal ranges, *P. cinctus* being the most northerly and *P. palustris* the most southerly, both overlapping with *P. atricapillus,* whose latitudinal range is intermediate. In table 1 the wing/tail ratios of these three most widespread species are shown for Scandinavia, Siberia and an extreme southwestern locality. The southerly *P. lugubris,* from south-western Asia and south-eastern Europe, agrees with the general trend in its relatively short tail (85–87%), and of the two restricted Asiatic species, *P. davidi,* which occurs in the subtropical forest zone of the mountains of western China and eastern Tibet, has the shortest tail of all (76%), while *P. superciliosus,* which occurs in the same region very high up, above the conifer forest, has the longest tail (102%). Similarly *P. cyanus,* from Siberia and central Asia, has a longer tail than the closely related *P. caeruleus,* from Europe. It thus seems certain that a long tail is an adaptation to a cold climate, though the reason is obscure. A comparable situation within the tropics has been found by Longhurst (1952). He has found that birds from Java tend to have relatively longer tails than birds of the same species from Borneo, which has a wetter and probably rather warmer climate.

GEOGRAPHICAL VARIATION IN BEAK- AND TARSUS-LENGTH

In nearly all the species of *Parus* which have been investigated in enough detail, the lengths of beak and tarsus have been found to vary in accordance with Allen's rule, i.e. they are relatively shorter in the colder parts of the range of the species. The most complete data are available for *P. major* and *P. caeruleus* (fig. 4). In these species it has been found that the reduction in length with decreasing temperature occurs only in the higher tem-

perature-ranges; below a certain temperature the relative length remains about the same. This suggests that Allen's rule involves a progressive departure from the mechanically efficient state, and that at a certain point selection for efficiency of feeding (in the case of the beak) or movement (in the case of the tarsus) overrides selection by minimum temperatures.

Interspecific comparisons support this hypothesis. If closely related species are compared in regions where they occur together, relative beak-length and relative tarsus-length tend to be shorter in the more southerly than in the more northerly species (table 2). The former is of course nearer the northern limit of its range. It seems in fact as if adaptation to a very cold climate must involve some degree of emancipation from Allen's rule. The situation is the same as that found in examining size trends: reproductive isolation of species or sections of species allows the adjustment of the genotype so as to maintain the dimensions that are adapted to their ecological niche, whatever the conditions of climate under which they may live.

Geographical Variation in Colour

Subspecific correlations between colour and climate have been found to be general. In species with a predominantly brown colouration, browns are paler and greyer in cold climates, darker and usually more rufous in warm and humid climates. In species with grey, blue-grey or green backs, back-colour is paler and greyer in cold, arid climates, darker and more olive in warm, humid climates, and darker and bluer in warm, arid climates. Yellow pigment, whether present as a constituent of back-colour or on the under parts, decreases with increasing aridity and cold. Whites are purer and more extensive in cold climates, a tendency that may be reflected in a paler general colouration, as above, or in more extensive white edges to wing and tail feathers or more extensive white check-patches. There is a tendency towards an increase in the amount of glossy black in warm climates.

The same trends are seen when comparisons are made between closely related species. Thus *P. cyanus,* from cold central Asia and Siberia, differs from *P. caeruleus* in its much paler colour, extensive white on wing and tail, and absence or extreme reduction of yellow. In the *Poecile* group, the closely related *P. palustris* and *P. atricapillus* differ from one another in accordance with the trends outlined above: where they occur together, *P. atricapillus,* the more northerly species, is paler and greyer, with a less glossy cap, more extensive white cheek-patches, and whiter edges to wing and tail feathers. But *P. cinctus,* the most northerly species, which belongs to the same group but is evidently not very closely related to the other two, is actually browner than they are, though it agrees with the general trend in entirely lacking all black.

When comparisons are made between all the species of the genus, the tendency to an increase in the amount of glossy black in warm climates is striking. In many tropical and subtropical species (especially *P. nuchalis, P. monticola,* the *Pardaliparus* and *Machlolophus* groups and the African species), parts of the plumage which in Palaearctic species are

Table 2. *Ratio of beak-length and tarsus-length to wing-length in* P. atricapillus *and* P. palustris (Wing-length is accepted as unity in each case)

		England	S. Scandinavia	Lapland	W. Siberia	E. Siberia
Beak	*P. atricapillus*	0.18	0.17	0.17	0.17	0.16
	P. palustris	0.17	0.16	—	—	0.15
Tarsus	*P. atricapillus*	0.28	0.25	0.25	0.25	0.24
	P. palustris	0.26	0.25	—	—	0.23

grey, brown or olive-green are either wholly glossy black or mottled with black.

In some of the isolated populations into which several of the species are split, correlations with climatic differences have not been found. This is particularly well illustrated by *P. ater,* which has a number of very distinct subspecies isolated in montane forest regions of the southern Palaearctic Region, from the Atlas Mountains in the west to China and Formosa in the east; while, by contrast, northern Palaearctic populations of *P. ater,* which have a continuous distribution from east to west, show great uniformity, with a little clinal variation in accordance with the climatic rules. In such cases it is often difficult to see any adaptive significance in the colour differences, as has often been pointed out for other genera (e.g. Mayr, 1942). They offer a special problem, on which the present study has thrown no new light. It may be stressed, however, that these unexplained colour differences are in sharp contrast to the regular and predictable colour-trends in continuous populations, suggesting adaptation to different environmental factors.

Unmodified and Modified Adaptations to Climate

The variations that have been described fall into two categories, which seem to represent two types of adaptation to climate. With respect to relative tail-length and colour, variations in relation to climate may be regarded as adaptations carrying with them no concomitant disadvantage, and comparisons between species show the trends in more extreme degree than comparisons between subspecies. With respect to size, tarsus-length and beak-length, however, Bergmann's and Allen's rules tend to produce departures from the state best adapted to the ecological niche: the evolution of distinct groups (species or isolated sections of species) may involve an adjustment of the gene-complex so that in spite of climatic differences the most efficient size, or length, is maintained as far as possible in each group. Thus when closely related groups are compared, it is found that the average lengths of wing, tarsus and beak are rather constant, whatever the climatic ranges.

Adaptations to Other Environmental Factors

In a genus like *Parus,* where so much of the geographical variation is related to climate, adaptations to the biotic environment are bound to be less evident. Thus the potentially cryptic back-colours of most of the species seem at first sight as if they might represent adaptations to the predominating colour of the habitat, but no evidence that this is in fact so has been discovered, and in some cases it seems very unlikely that it could be so. For instance, the back-colour of *P. atricapillus* across the taiga belt of the northern Palaearctic varies clinally from grey-brown (in the west) to a very pale grey that is almost white (in the east), while its habitat remains essentially the same in appearance. Adaptations to the superficial colour of the habitat would be expected frequently to obscure or even obliterate these climatic trends, but they do not. In fact, if colour were adapted to some factor of the biotic environment, modifications due to the climatic rules would to that extent be disadvantageous, and one would expect the climatic colour-trends to be of the "modified" type, as are those of size, beak-length and tarsus-length.

In the same way, regional differences in structure or colour must be examined carefully in this genus before they can be attributed to interspecific competion. It has been suggested (Lack and Southern, 1949) that *P. caeruleus* in the Canary Islands shows convergence in its long beak and blue-grey back to *P. ater,* the species which in Europe is normally found in the sort of conifer forests inhabited by *P. caeruleus* in some of the Canary Islands. But the long beaks (and also the long tarsi) of *P. caeruleus* in the Canary Islands represent the end-terms of a cli-

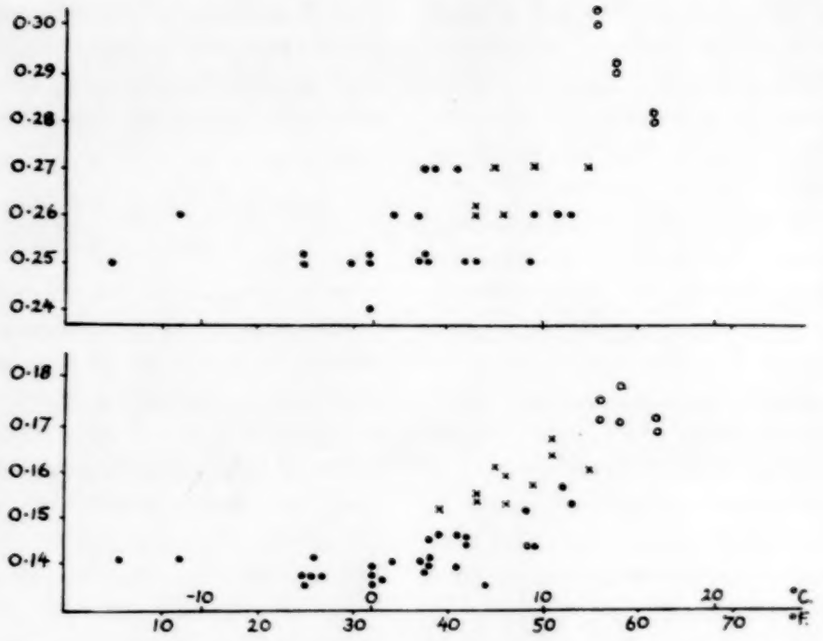

FIG. 4. Relation between relative tarsus-length (top) and relative beak-length (bottom) and the mean temperature of the coldest month in *P. caeruleus*. Dots: European section. Crosses: North African section. Circles: Canary Islands section.

matically-related trend of increasing relative length (fig. 4). It is essentially the same as is found in other species, but more pronounced because *P. caeruleus* alone reaches the very warm Canary Islands, where total isolation from more northerly populations prevents any damping-down effect from gene-flow. The blue-grey back-colour similarly follows climatic trends that are general throughout the species—reduction of lipochrome and increase of melanins in warm and arid climates.

No external subspecific differences in any of the species examined have in fact been satisfactorily attributed to the presence or absence of another species of the genus. However, in the case of the two most similar of (partially) sympatric species in the Palaearctic Region, *P. palustris* and *P. atricapillus*, there is evidence that in certain areas where *P. atricapillus* is absent *P. palustris* has occupied its typical habitat (e.g. in Denmark, the Caucasus, Korea and southeastern Asia, where *P. palustris*, elsewhere more or less strictly confined to broad-leaved woodland, is found in coniferous woodland, the characteristic habitat of *P. atricapillus* over almost the whole of the northern Palaearctic Region). With other pairs of species this has not been found, although there are many opportunities for such changes of habitat. It is concluded that most Palaearctic species of *Parus* are now too specialised ecologically for the local presence or absence of one to affect the colour, structure or ecology of the other. It is noteworthy that the well authenticated cases of such an effect (*Fringilla coelebs* and *F. teydea* in the Canary Islands (Lack and Southern, 1949), *Sitta neumayer* and *S. tephronota* in Persia (Vaurie, 1951)) concern species more similar to one another than are any of the sympatric Palaearctic *Parus* species, with the possible exceptions of *P. palustris* and *P. atricapillus*.

PARALLEL EVOLUTION DUE TO SIMILAR CLIMATES

When, as in the genus *Parus*, geographical variation is closely connected with climate, it is to be expected that more

or less complex contour systems will be set up for each character whose variation is correlated with climate, and that similar populations, evolved in areas with similar climates, will often be separated by dissimilar populations in intermediate areas where the climate differs. Figure 5 shows the contour system which, on the basis of the material examined by the writer, represents the geographical colour variation (but not the size variation) of *P. cristatus*: the other brown-backed European species (*P. palustris* and *P. atricapillus*) show a rather similar pattern of colour variation, allowing for differences in their ranges.

Although this kind of parallel evolution is well known, some bird systematists, when working out evolutionary or distributional histories of genera, still tend to use quite minor differences in colour and size as clues to past history (most recently Voous and Van Marle, 1953), postulating a common phylogenetic origin for similar populations and thus coming to conclusions about such things as glacial refuges and postglacial spread. The situation in *Parus* shows that an examination of the relations between colour and structure and present-day environmental factors such as climate should be an essential prerequisite of any investigation of the evolutionary history of a genus.

Summary

1. In the genus *Parus* in the Palaearctic Region geographical variation is closely related to climate. Bergmann's rule is general, but it is modified to a greater or lesser extent by a "latitude effect," size being greater at lower than at higher latitudes for equivalent winter temperatures. In nearly all the species, relative tail-length increases and the relative lengths of beak and tarsus decrease in the colder parts of the range (Allen's rule). In continuous populations colour variation follows differences in temperature and humidity.

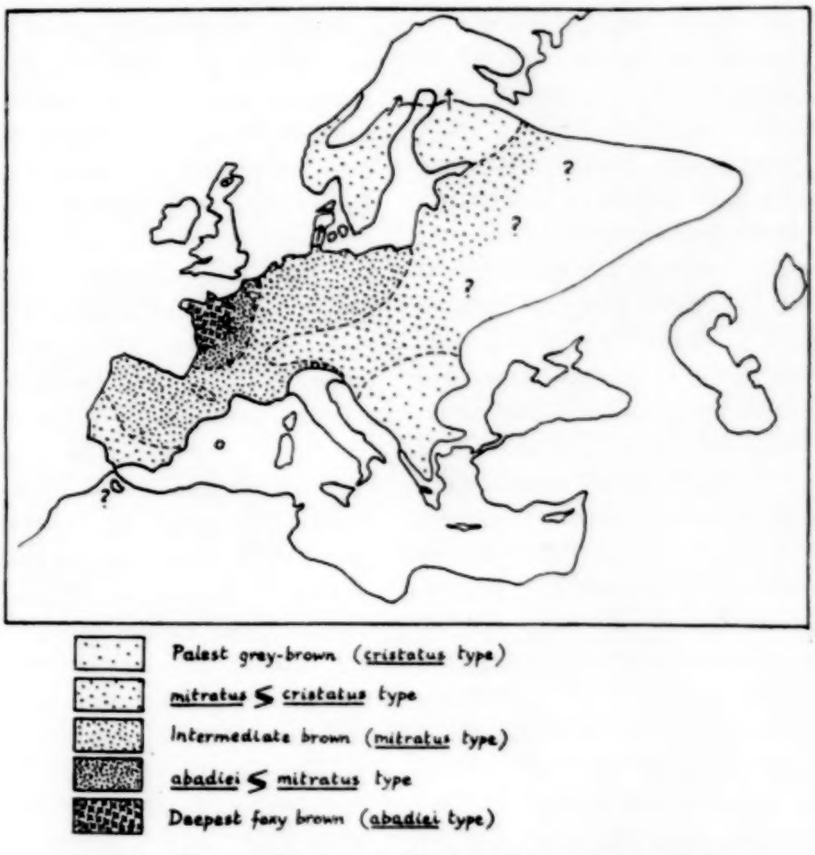

FIG. 5. Geographical variation in colour in *P. cristatus*.

2. The rules for variation in colour and tail-length seem to carry with them no concomitant disadvantages, but Bergmann's and Allen's rules may at times conflict with other ecological requirements.

3. Until the geographical variation of a whole genus has been analysed with respect to climate, subspecific differences cannot be safely interpreted as adaptations to habitat or to the presence or absence of competitors, nor can they be used as clues to past history.

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PHYSIOLOGICAL PROPERTIES OF GENE ARRANGEMENT CARRIERS IN *DROSOPHILA PERSIMILIS* III. CYTOPLASMIC INFLUENCE ON FECUNDITY OF ARRANGEMENT HETEROZYGOTES

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INTRODUCTION

Competition experiments utilizing artificial populations designed to measure adaptive values of chromosomal variants from various *Drosophila* species have demonstrated in many instances that each arrangement from any particular locality at a single point in time may possess particular genetic properties maintained principally by the action of natural selection. Such genetic properties often must be perpetuated by a co-adaptation between two separate arrangements, that is, by the incorporation of higher net fitness in arrangement heterozygotes (Wright and Dobzhansky, 1946; Dobzhansky, 1952).

In seeking for physiological properties which are determined by the gene contents of certain chromosomal arrangements from *D. persimilis* native to the Yosemite area of California, the author has found that the properties of the two most common arrangements (Whitney and Klamath of chromosome III) generally differed when comparing homozygotes, and heterozygotes often displayed heterosis (Spiess, Ketchel, and Kinne, 1952: Spiess, Terrile, and Blumenheim, 1952).

It was in the egg-laying capacity experiments that a number of interesting facts lending support to expectations from competition experiments appeared (Spiess, 1950). 1) Flies homozygous for Whitney or Klamath differed in fecundity; 2) heterozygotes maintained a higher rate of production than either homozygote but differed in their production depending upon which arrangement was derived from the female parent. This difference in reciprocally derived heterozygotes though slight was nevertheless significant. Apparently while increased egg production was characteristic of the heterozygotes, an influence from cytoplasmic factors conditioned by the chromosomal arrangement of the female parent effected a detectable amount of difference in expression of heterosis. It was decided to test further this cytoplasmic conditioning effect in inversion heterozygotes by measuring the egg-laying capacity of Standard arrangement females and their heterozygotes with Whitney.

MATERIALS AND METHODS

The techniques employed were substantially the same as those used in the WT–KL tests (see Spiess, Ketchel, and Kinne, 1952), except that females tested were the strain cross progeny of single pair matings rather than of mass matings. For each chromosome combination either three different strains of each gene arrangement were mated in combinations as A × B, B × C, and C × A; or where only two strain crosses were made, the combinations involved three strains as A × B and B × C. Homozygous females tested were strain cross F_1's while heterozygous females were produced by mating F_1 individuals from different strain crosses. These preparations were necessary to make the tested individuals genetically heterogeneous but cytologically homogeneous. At least ten and no more than thirty females from each strain cross were used. All tests were carried out at 16° C.

Each female to-be-tested was mated in a glass vial, and food was introduced on a plastic spoon. Spoons were changed

every other day, and eggs laid in the two day period recorded. Flies laying less than ten eggs in a week's time after the first egg laid were not tabulated. All flies were derived by mass matings from strains native to Jacksonville, California, collected there by Professor Carl Epling in February, 1948.

Experimental Results

In table 1 are recorded the results for the three zygotic combinations, and several facts seem to be apparent:

1) ST/ST equals or produces slightly more eggs per day than WT/WT in the first ten days of laying but as a group decreases slightly in the second period of fifteen days. It was decided not to carry out the tests after the twenty-fifth day since it was already known from the WT–KL tests that differential production would be evidenced in early periods and less in senescence (Spiess, Ketchel and Kinne, 1952). In contrast WT/WT maintains its initial production for the entire period of twenty-five days. Attention should be called also to the fact that WT/WT averages approximately 20 eggs per day in these tests whereas in the WT–KL tests referred to above WT/WT averaged about 15 eggs per day: these latter tests were made on females reared in very crowded conditions (population cages or mass matings) while the present reported tests were made on females reared from single pair matings in half-pint bottles. Since egg-laying capacity is remarkably constant under a given set of conditions, it appears that one condition affecting rate of production is availability of space and food as determined by population density during development. ST/ST contrasts sharply with KL/KL in respect to WT/WT (which can be considered as reference) in that ST/ST is equal or superior to WT/WT while KL/KL was slightly inferior in the first period of ten days but a considerably poorer egg-layer following the initial ten day period of laying.

2) Heterozygotes derived from WT mothers have egg-laying capacity equal to that of WT/WT for the entire period of twenty-five days, but those derived from ST mothers produce at a rate approximately half that of their reciprocals. For these latter heterozygotes, however, a significant increase in eggs per day appears in the second period from eleven to twenty-five days, an increase which as a group does not reach the rates of the other zygotic combinations.

Table 1. *Egg-laying capacity of flies given in average number of eggs per day for genotypes: WT/WT, ST/ST, and WT/ST (Jacksonville, California).* Column ## refers to experiment consisting of uniform progeny derived from one strain cross.

Genotype	##	First 10 days	11–25 Days
ST×ST	C	21.2±1.11	19.9±0.65
	E	23.7±0.85	17.3±0.74
	E (repeat)	23.1±0.80	19.8±0.58
WT×WT	B	19.1±1.70	—
	K	21.1±0.91	21.0±0.65
WT/WT female× ST/ST male	G	17.9±0.94	—
	J	20.9±0.87	20.7±0.45
ST/ST female× WT/WT male	F	11.9±1.15	16.2±1.78
	I	10.1±1.51	16.4±1.23
	H	10.5±1.26	19.4±0.77

Discussion

One interesting aspect of these results lies in the fact that they were just the reverse of what was expected from artificial population studies of competition between these two arrangements. In the studies of Spiess (1950) with ST and WT flies from Jacksonville, California, at 16° C. equilibrium occurs at about 80% WT–20% ST. Clearly from the concepts of Wright (1931) the order of adaptive values for the three zygotic combinations concerned must be WT/ST > WT/WT > ST/ST. If the first period of egg-laying alone is considered it is quite obvious that the result is opposite from the expectation. Heterozygotes are inferior slightly or

greatly depending on the parental genotype, a "reversed" heterosis, while ST/ST flies produce better than or equally with WT/WT. It is difficult to visualize how decreased egg production could be adaptively superior to high egg production. There remain possibilities not yet tested that hatchability and survival of larvae may be proportionately greater in the heterozygote. Certainly egg-laying is only one of countless functions which might have adaptive significance, and apparently by itself does not contribute any positive net fitness as far as WT/ST is concerned.

From the genetic point of view the reciprocal effects found for WT–KL and WT–ST heterozygotes is of somewhat greater interest. The fundamental mechanism of hybrid vigor obtained in F_1's of inbred strain crosses has been determined as a nuclear phenomenon. The work of Gowen, Stadler, and Johnson (1946) on *D. melanogaster* comparing the egg-laying of inbred stocks with that of homozygous flies obtained by an outcrossing technique to a multiple marker stock has done much to reduce the probability that cytoplasmic interaction following fertilization can account for any but a small portion of hybrid vigor. Certainly by studies of egg-laying Gowen and his students have shown increased egg production in hybrids to be due to chromosomal differences in the parents (Gowen, 1952).

Nevertheless it is reasonable that female nuclear gene products may enter the cytoplasm of the egg which in turn can interact with heterozygotic nuclear products in such a way as to intensify or suppress the vigor arising from the nuclear elements. The evidence here presented can be interpreted by assuming such a conditioning of the egg cytoplasm before fertilization. Presumably genes on the third chromosome must bring about the conditioning either from intracellular products of the egg nucleus or from products added by nurse cells surrounding the ovum. Whichever is the case at any rate genes in the zygote nucleus interact with these cytoplasmic products presumably in such a way that the characteristics tested are suppressed or intensified depending upon the nuclear genotype of the parents.

Reciprocal effects on heterotic characteristics have been observed many times but in general the effects have been slight or non-significant. Jones (1952) mentions two cases which are relatively important: two different flowering types of tobacco show significant reciprocal differences in height of F_1, and crosses between California Rice pop corn and inbred Indiana Wf9 display differences in early seedling growth and in tillering depending on which type is the maternal parent (greater number of tillers and more rapid early development when Wf9 × Rice pop than the reciprocal).

Gowen points out that when egg productions of several inbred races and their first generation hybrids are analyzed the amount of variation contributed by reciprocal effects is negligible (about 2.3%). Such a result for *D. melanogaster* contrasts markedly with that found so far with *D. persimilis*.

Summary

1) *Drosophila persimilis* homozygous for the Whitney or Standard gene arrangements of the third chromosome do not differ significantly in egg-laying capacity although ST is a slightly better layer as a group than WT at 16° C. under optimal conditions for an initial period of ten days. Thereafter ST drops slightly as a group on the average of 2–4 eggs per day below the initial period.

2) Heterozygotes from WT mothers maintain a production equal to or slightly less than WT homozygotes throughout a twenty-five day period. However, heterozygotes derived from ST mothers produce at a rate approximately half that of their reciprocals during the initial ten day period followed by a decided increase of 6–9 eggs per day during the second period of two weeks.

3) The contribution of egg-laying to the positive net fitness of WT/ST is doubtful since it is difficult to visualize

how decreased egg production could be adaptively superior to high production.

4) Since a reciprocal effect on egg-laying has been found both for WT/KL and for WT/ST it is reasonable to postulate a conditioning of egg cytoplasm by female nuclear gene products before fertilization and resulting in zygote nucleus interaction with these products in such a way that the characteristics tested are suppressed or intensified.

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EVOLUTION OF FEEDING PREFERENCES IN PHYTOPHAGOUS INSECTS

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The extent to which biological races represent a transient stage in the evolution of species, especially among insects, has been the subject of extended discussion ever since the existence of these categories was first demonstrated by Walsh in 1864. It is considered by many that isolation, at least to some extent, by host preferences is a *sine qua non* for biological races (Thorpe, 1930; Mayr, 1942; Huxley, 1942). With such emphasis placed on host preference it is indeed surprising that only comparatively meagre attention has been directed toward the physiology and evolution of host habits. A thorough analysis of the problems of host selection would appear to be a logical prerequisite to an intelligent understanding of the role of biological races in evolution. This review has been undertaken in the hope that it will reveal in some measure the lacunae as well as the matrices in our knowledge of one well known aspect of host selection, namely, the host preferences of plant feeding insects.

I

Conceive, for the moment, of an organism as a complicated biochemical machine surrounded by a hostile environment. It may isolate itself completely and remain quiescent for long periods of time as do seeds, animal spores, and certain diapausing insects. Under these conditions energies are directed toward maintaining the *status quo*. If the organism is to accomplish anything beyond static existence, and is to reproduce, there must be energy transfers across the surfaces separating the internal from the external environment. And this too requires energy. If an organism is small and content to sit in one place taking in energy in the form in which it is to be found there and dying when the supply is exhausted, then the principal, and practically only, requirement for existence is a selectively permeable surface through which the environment cannot act adversely. From passivity to aggressiveness is a step which involves food procurement and locomotion. Execution of these accomplishments in turn requires a signal system, coordinating mechanisms, and further complexities.

With the acquisition of mobility, animals also acquired the potentialities for expanded opportunities for self selection of diet, a talent which is largely denied to sessile organisms and constitutes no problem for dormant ones. Sessile marine organisms, for example, can select only from those food substances which the environment transports to them. Among sessile species some, such as sea anemones, do indeed exercise a degree of selection (Pantin and Pantin, 1943). Other species, notably cockles, oysters, and mussels, are generally believed to ingest indiscriminately all particles whose size permits handling (Verwey, 1952).

Throughout the animal kingdom the selection of diet has become most highly developed among mobile species. It has attained finest discrimination among parasitic forms and, of free-living species, among those insects which feed upon plants. Plant feeders account for approximately fifty per cent of living insect species. In no other groups of animals are feeding preferences so sharply delineated. The questions as to the origins and evolution of these precise relationships existing between certain phytophagous insects and their host plants are indeed thorny ones. Until recently the mecha-

nism underlying food preference and the directing forces operating in the execution of the relationship were poorly understood and a matter of considerable speculation. Now with a clearer understanding of these factors it is possible to scrutinize more intelligently the mass of records of insect/plant relationships which have been bequeathed to us by scores of field entomologists and to derive from this midden of notes some inkling of the direction which the development of intimate insect/plant biocoenoses may have taken.

Considered solely from the point of view of energy source, organisms are limited only by their biochemical inadequacies, and among heterotrophs the capabilities of utilizing energy sources under a multiplicity of forms are such that the majority of heterotrophs are potentialy omnivorous. In seeking to understand the fact of diet selection the questions then arise: (1) do the various species of phytophagous insects have different nutritional requirements? (2) are the preferred plants superior from the nutritive point of view? (3) is the underlying basis of plant preference a nutritional one? These are extraordinarily difficult questions to answer unequivocally because our knowledge of the nutrient requirements of phytophagous insects and of the food value of different plants and of the same plant under varying conditions is pathetically scanty. It must be emphasized that there is a vast difference between the food ingested and the nutrients actually required and utilized. It is an all too common mistake to equate gross food intake and utilizable constituents (cf. Uvarov, 1928).

Even a reasonably complete understanding of the nutritional requirements of phytophagous insects is not now enjoyed (Uvarov, 1928; Trager, 1947; Fraenkel, 1953). Of those insects which have been studied more or less intensively, *Tribolium confusum, Tenebrio molitor, Ephestia kuehniella, Blatella germanica,* and *Drosophila melanogaster* are remarkably similar in their requirements. All require an adequate supply of amino acids, a sterol, eight to ten of the known B vitamins, carbohydrate in readily available form, and a number of minerals (cf. Trager, 1947 and the papers of Fraenkel and Leclercq). Insects differ in their quantitative and qualitative requirements for carbohydrate and do not as a rule require fat (Fraenkel, 1953). The most successful of the few attempts to feed leaf-feeding forms on a synthetic diet was that made with corn borer larvae (*Pyrausta nubilalis*). These grow well on glucose, casein, cholesterol, corn oil, minerals, yeast, choline, and lyophilized corn leaves. Growth is reduced in the absence of leaf preparation and with yeast replaced by pure B vitamins (Beck, Lilly, and Stauffer, 1949).

Notwithstanding the scanty knowledge at present available to us it appears unreasonable to imagine that the basic requirements of the different phytophagous species are not essentialy the same, or that the enzyme systems of polyphagous forms differ radically from those of strictly monophagous forms (cf. Brues, 1920). Perhaps there exist quantitative differences which reflect different degrees of efficiency in the utilization of available materials. It is a fact that phytophagous insects as a group do not practice economy of feeding. From one half to two thirds of the food is eliminated as feces. Most of the protein, fat, and simple carbohydrate may be utilized; but starch and cellulose are excreted mostly unchanged (Fraenkel, 1953). Chlorophyll is degraded but apparently not used. The waste is strikingly illustrated by the recent work of Gray (1952), who has shown that the pineapple mealybug, *Pseudococcus brevipes,* secretes in its honeydew large amounts of as many as nine different amino acids and amides. The number of amino acids secreted increases as feeding is increased. Excess carbohydrate is not, therefore, ingested merely as incidental to an attempt to insure an adequate protein supply.

On the other hand, under threat of impending starvation many insects tend toward wider polyphagy and can survive on the altered diet (Brues, 1939). Furthermore, as Dethier (1947) and others have pointed out, even insects with restricted diets can, by various experimental artifices, be induced to feed successfully on foreign food plants.

As far as can be judged from available data, leaves possess ample supplies of the essential nutrients (Fraenkel, 1953), and there are not great differences from one species to the next. It is not known to what extent optimal concentrations vary with season, growth stage, soil, etc. These changes have been studied intensively only in a few agricultural crops (and mulberry). In the other few species investigated the changes have been studied exclusively with respect to specialized compounds such as lignin, carotenoids, and essential oils (Guenther, 1948). Fraenkel (1953) considers that evidence is lacking to the effect that seasonal changes in plants are of great importance in the nutrition of insects. Fennah (1953), on the other hand, maintains, at least insofar as Homoptera in the humid areas of the Neotropical region are concerned, that the qualitative composition of food solutes is not constantly optimal and that *relative* abundance of nitrogen, carbohydrate, and mineral fractions (i.e., the overall metabolic rate of the host plant) is of greater importance than such gross factors as total nitrogen or carbohydrate or even the C/N ratio.

The criteria customarily accepted in assessing the nutritional value of food are growth, development, longevity, fecundity, and population density. On these bases there can be no doubt whatsoever that certain species, varieties, and organs of plants serve the growth and reproductive requirements of particular insects more effectively than do others. The facts are amply documented that the duration of immature stages of insects fed on unfavorable plants may be greatly extended, that insects may pupate before maximum growth has been attained, with the resultant production of runts, that mortality increases to varying extents, and that fecundity may decline and population density decrease (Painter, 1951; Fennah, 1953; Kennedy, 1953). In certain specific cases the failure of insects to maintain themselves has exhibited a distinct correlation with the presence or absence of specific compounds in the plant. For example, a low concentration of linoleic acid in some food plants of the sugar beet webworm (*Loxostege sticticalis*) has been associated with infertility of females which fed thereon as larvae (Pepper and Hastings, 1943). Deposition of lignin and pentoses in alfalfa under altered conditions of light and moisture has paralleled reduced feeding on the part of the pea aphis, *Macrosiphum pisi* (Emery, 1946).

How directly the aforementioned manifestations reflect the nutritional adequacy of the plant is a matter of considerable doubt. They do not prove (nor can the possibility be excluded) that optimum levels of nutrients vary critically from one species of plant to the next or within a species from time to time. In attempting to interpret observations such as these one must take into consideration the possible action of attractants, repellents, and toxins in influencing the quantity of food ingested. The study by Wagner (1944) of the feeding habits of *Drosophila mulleri* and *D. aldrichi* is a case in point. Several species of drosophilids feed in the cactus *Opuntia lindheimeri* but actually subsist upon the various microorganisms, especially yeasts, found in the cactus. Of the yeast species present, nine supported the growth of *D. mulleri* but only six were satisfactory to *D. aldrichi*. This result by itself is not prima-facie evidence of a difference in the basic nutritional requirements of the two drosophilids.

Dethier (1947) and Fraenkel (1953) believe that nutritionally unimportant token stimuli (attractants and repellents) are predominantly responsible for regulating the feeding preferences of phy-

tophagous insects. Kennedy and his coworkers (1950–1953) and Fennah (1953), on the other hand, are of the firm opinion that the relation between preference and nutritional requirements, especially as it applies to tissue preference, is of a more causal nature and of considerably more importance than heretofore acknowledged. Kennedy has investigated in great detail, chiefly with respect to the differential suitability of leaves of a single plant, the feeding preferences of two species of aphids, the black bean aphis (*Aphis fabae*) and the peach potato aphis (*Myzus persicae*). Both of these insects feed preferentially on young growing leaves and old senescing leaves, on both customary hosts and unusual hosts. There is an active behavioral preference for these leaves quite in addition to a species discrimination. Physical stimuli are not involved, olfactory may be, and gustatory most certainly are (cf. Fife and Frampton, 1936, and Day and McKinnon, 1951). While fecundity is admittedly not an accurate index of the actual nutrient value of the food ingested (since there is no control over the quantity ingested), the fact that fecundity differences correlated more directly with leaf age within a plant than with plant species difference has prompted Kennedy (1953) to argue that the factors mediating intraspecific preferences are fundamentally different from those operating in the case of interspecific preferences. Both involve behavioral discrimination, but the former has been termed a "nutrient" discrimination in that, it is postulated, *A. fabae* reacts behaviorally to certain nutrients or compounds associated with them. The actual involvement of nutrients requires proof. It has been noted that the two aphis species behave differently in that the physiological ages of the prefered leaves differ slightly. Also, there appear to be differences in the behavior of alatae and apterae (Kennedy *et al.*, 1950). If the preference is so entirely a question of nutrition, then these different species and different forms must have slightly different nutrient requirements.

It is suggested (*loc. cit.*) that one set of compounds may be involved in differentiating plant species and another in leaf age differences. This concept would certainly agree with evidence from other quarters (Dethier, 1953). It would harmonize with the idea that one set of compounds subserves elaborate ecological differentiation and the other a more probably uniform nutritional requirement. A tentative alternative explanation may be offered, namely, that these aphids are essentially polyphagous, attacking any available plant species not containing repellent or toxic compounds, and that leaf age preferences are governed by one or more compounds acting on a contact (gustatory) chemical sense. These may or may not be directly related to nutrition. Such an interpretation would not disagree with the observation that *A. fabae* appears to discriminate more sharply between leaves of the same plant than between leaves of two plant species (Kennedy and Booth, 1951).

Thus, while the recognition of food by nutritionally unimportant token stimuli is certainly well established (Fraenkel and Gunn, 1940; Dethier, 1947, 1953; Tinbergen, 1951; Thorsteinson, 1953), the relation between nutritionally good and sensorially attractive materials remains an open question. It is clear that the four relevant properties of a host plant—odor, taste, toxins, nutrients—occur in varying combinations, as Chin (1950) has shown for Solanaceae (cf. also Fennah, 1953). Kennedy is of the firm opinion that it is improbable that these vary randomly or that insects always react to tokens which may only happen to be associated with nutrients. Yet it has been amply demonstrated that all nutrients are not stimulating and that some compounds which are eminently acceptable to insects are nutritionally inadequate (Vogel, 1931; von Frisch, 1934; Trager, 1947; Hassett *et al.*, 1950).

It is when the selection of plants by the ovipositing female of holometabolous insects is considered that a predominantly

nutritional approach is most difficult to invoke. The female selects a plant or part thereof which is to feed the larvae and is not at all the proper food for herself. In the case of gall insects and certain miners whose presence in the plant tissue stimulates that tissue to growth which is said to be high in nutrients, it can hardly be argued that the plant or tissue is chosen initially on a nutritional basis since the choice is made before the hypertrophy commences. An outstanding instance is that of certain single-tissue leaf miners in which oviposition on the top surface of a leaf leads the larva to mine in the nutritionally preferred palisade layer, and an egg on the under surface presents the emerging larva with the disadvantage of mining in the nutritionally inadequate spongy parenchyma (Hering, 1926). All of these lines of evidence indicate convincingly that nutrition is not the *prime* directing principle underlying preferential feeding. The failure to survive and reproduce on various plants cannot be construed *ipso facto* as indicative of nutritional deficiency. As will be shown below, behavioral factors and toxic principles play a considerable part.

We must, then, seek elsewhere for purposes served by food plant preference. Obviously, it is ecologically expedient that some specialization of feeding habits exist. From the point of view of species competation there are advantages in filling all ecological niches so that as many plants as possible serve as host plants. This would be accomplished if all insects were unrestrictedly polyphagous, but viewed in terms of interspecific competition polyphagy is distinctly inferior to monophagy or oligophagy. To just how great an extent competition varies with the number of species restricted to a give food is a problem concerning which few pertinent data are available. Numerous studies have been made of protozoa (Gause, 1934, 1937) and of predatory birds (e.g. Cushing, 1944) but few of insects (cf. Park, 1941; Wagner, 1944; Crombie, 1945; Solomon, 1949). Some of the observations made of birds are particularly pertinent. Lack (1949) has observed that closely related birds living in the same habitat differ in diet, that two monophagous species cannot persist if they compete for the same diet, that polyphagous species living in the same habitat frequently show an overlap in diet. Amadon (1950), in speaking of the Hawaiian honeycreepers, has pointed out that where species *a* alone occupies an island it has generalized feeding habits but where it shares an island with species *b* each has a restricted diet.

Indirect evidence of the value of restricted feeding is seen in the numerous examples of widespread, although not invariable, specialized sharing of the environment (Huxley, 1942). Rather extensive data relating to butterflies of the genus *Colias* have been gathered by Hovanitz (1949, 1950). In North America, *C. philodice,* feeding on *Trifolium,* overlaps geographically and ecologically with *C. eurytheme,* feeding on *Medicago; C. christina,* feeding on *Astragalus* and other legumes, overlaps with *C. gigantea,* feeding on *Salix; C. hecla,* feeding on *Astragalus,* with *C. nastes* on *Astragalus* and *Trifolium; C. interior* on *Vaccinium,* with *C. philodice* on *Trifolium. C. palaeno, C. interior, C. pelidne,* and *C. behri,* all feeding on *Vaccinium,* show some overlap but also considerable geographic replacement. In the butterfly genus *Basilarchia* the species *B. archippus* overlaps the range of each of the four remaining species (Hovanitz, 1950). The food plants are identical for four of the five species. Among copper butterflies of the genus *Lycaena, L. hypophlaeas,* feeding on *Rumex,* overlaps in the eastern United States with *L. epixanthe,* feeding on *Vaccinium* and with *L. thoe,* feeding on *Rumex.*

Polyphagy is a luxury which can be enjoyed under certain conditions only. Among its obvious advantages are the lack of complete dependence upon the fluctuating fortunes of a single plant species and, too, at least superficially, better potentialities for world-wide distribution. Monophagy is a realistic solution to the prob-

lem of species pressure. It too permits of world-wide distribution if it is associated with a cosmopolitan plant. The milkweed butterfly (*Danaus plexippus*), which in North America feeds exclusively on *Asclepias,* is an outstanding example of a restricted feeder of wide geographical distribution.

The very apt statement of Kennedy (1953) that "the favoured host plant is not merely something fed on, it is something lived on" suggests other services rendered by preferred food plants. The plant is accepted with its microclimate, its shelter, its predators, its diseases. A whole community is selected. Comparable instances of habitat selection by vertebrates are well known (Miller, 1942). Finally the plant is not a passive partner to the association. It also plays a part in preference, responding as an organism and developing protective mechanisms which interfere with the utilization of its tissues as food by insects. This aspect of preference has been expounded at great length by Painter (1951) in his book on plant resistance. In short, the course of development of food plant preferences involves simultaneous evolution of resistant mechanisms by plants and of tolerance and preference by insects so that the picture at any time is one of dynamic equilibrium moving toward a perfect symbiotic relationship.

When we consider the foregoing facts, it is apparent that we should not expect *a priori* a close correlation between nutrition and plant preferences. The end served by food plant preference is neither solely nor primarily a nutritive one, and in order to appreciate the evolutionary trends in feeding preferences it is desirable to inquire first into the mechanism of the phenomenon.

II

The whole problem of food plant selection may be stated in the form of two primary questions: (1) how is the preference implemented? (2) what is the genetic basis and evolutionary history of specific plant preferences?

As a fixed point of departure one can begin with the observation that insects as a group exhibit all degrees of preference from the polyphagous species which will feed on a vast number of plants to the monophagous species which restrict their feeding to a single plant species or variety, even to a specific tissue therein. As Brues (1946) has emphasized, however, there may exist among the most polyphagous forms marked preferences in diet (cf. also Koyama, 1951). The innate potential to choose diets thus appears to be common to most insects and differs within the class in degree only. Before considering the mechanism of plant selection, however, it is advisable to examine briefly and to eliminate some of those factors which influence superficially the expression of preference but have little or no direct bearing on the genetics of the performance or the immediate physiology of host selection.

To indicate that a plant is preferred is to imply in the broadest sense that it will support a population of insects and permit their propagation. From the point of view of an individual insect, however, a preferred plant may be one that is more acceptable even though nutritionally inadequate or highly toxic. In the latter instance a preferred plant is not to be confused with a susceptible one. Since the insect's death is hastened, the plant is protected, and such a plant is as much resistant as that which is unacceptable in the first place. The diverse qualities comprising resistance have been studied extensively by Painter, and the subject is excellently treated by him (1951) (cf. also Snelling, 1941).

Preference patterns are molded by geographical expediency, ecological variability, and seasonal cycles. It goes without saying that many plants might be eminently acceptable to a given insect were the geographical ranges of the two coextensive. This has been borne out by laboratory tests but even more spectacularly by the behavior of introduced pests,

which in various parts of the world have tasted and found to their liking plants not formerly available. It is noteworthy that very little thoughtful investigation has been directed toward the restraints imposed upon the ecological and geographical distribution of an insect by the range of its food plants (but see Huxley, 1942, p. 185; Wulff, 1943; Brues, 1946, p. 112; and Pfadt, 1949). Similarly neglected are considerations of the role which plant ecology plays in delineating food plant preferences. Of considerable import are the inequalities of microclimates within the area occupied by an insect or plant species (see, for example, Wolfe, Wareham, and Scofield, 1949). Thus, there are many plants which grow under such conditions of temperature, humidity, soil characteristics, and light as to place them beyond the pale for certain insects. And finally, unless the growing season of a plant coincides with the appearance of the feeding stages of an insect the plant obviously cannot serve as food. From the point of view of the plant the foregoing conditions have been termed evasion or pseudoresistance (Painter, 1936). In certain cases the preferences of an individual insect change with the season in accordance with the seasonal succession of plants. One very fine example is offered by the swallowtail butterfly *Papilio machaon* L., which, in desert areas, feeds on a succession of different host plants (Buxton, 1923).

Although the phenomenon of evasion plays a limited role in the objective expression of preferences, it sheds little light on the dynamics of selection. Given a number of available plants, preference operates by selection on the part of the insect. But in many forms preference, as far as the individual is concerned, is apparent rather than real. It fits only the broad definition stated previously. An insect population may initiate attack on a variety of plants indiscriminately and be unable to maintain itself because either (a) the plant chosen (randomly) was deficient in required nutrients, (b) contained toxic materials, (c) was protected by physical characteristics which impeded feeding, or (d) contained repellent compounds which mediated against feeding (cf. e.g. Ishii, 1951). Painter (1936) has classified *a* and *b* as antibiosis; *c* and *d*, as passive resistance. In all of these cases the population retires to a different plant lacking adverse characteristics or fails to migrate and is decimated. In the absence of migration, survivors might form the cadre which could develop by selection through successive generations a strain capable of surviving on the resistant plant. This end has been achieved several times experimentally (see Brues, 1924). In nature it is comparatively infrequent because insects usually desert an unfavorable plant or are completely wiped out. In any event, the final selection of a susceptible plant is by default and may be termed *passive selection*. Whereas this may have been the evolutionary forerunner of active selection (see p. 42), it is uneconomical to the species in the immediate sense since such passive selection is regulated by survival and involves high mortality.

Active selection, on the other hand, as with any self selection of diet, presupposes a means of recognition. While adult insects are at liberty to select their own diets, many larval forms are never granted this opportunity since they are restricted by spatial factors to the food selected by the ovipositing female. Such larvae, however, in common with those which employ a greater or lesser degree of foraging are none-the-less endowed with the ability to identify a preferred plant. Whereas this ability may serve no apparent useful purpose in the more sedentary forms, it is as essential to free foraging larvae as to adults. This is especially true in cases where the female may oviposit on the wrong plant, and many instances are recorded in which the range of choice of the ovipositing adult fails to correspond to that of the larvae (e. g. Salt, 1935). Then too, many species simply oviposit in the vicinity of the preferred food (e.g. *Argynnis*); and others,

such as some butterflies of the subfamily Hesperiinae, may eject eggs into space to fall by the wayside. It is imperative that larvae of these species be able to search for and recognize suitable food plants.

While vision, phototaxis, geotaxis, and hygrotaxis undoubtedly play a part in directing insects to the proper environment for oviposition and feeding, the ultimate forces working at close range are largely chemical (cf. Painter, 1936, and Dethier, 1947 for review and discussion of attractants and physical factors governing oviposition). In order to understand the mechanism of action of these, it is convenient to break down into three basic component parts the behavior pattern which culminates in normal feeding, namely: (a) orientation to the food, (b) biting response, (c) continued feeding. The entire complex is under the predominant control of the chemical senses, but each phase may be directed by discrete and different chemicals.

If the insect is not already in the proper feeding environment as a result of having emerged from eggs laid there, it is guided there by vision, light, gravity, and moisture. Final orientation to the plant or proper part thereof by monophagous and oligophagous species is effected by odors emanating from the plant tissues. In many polyphagous species orientation to the plant or proper tissue is, up to this point, random. At this time, in the usual course of events, a strong biting response is initiated by odor, contact chemical stimuli, or other less specific stimuli. The chemicals initiating these two phases of behavior may or may not be identical. Many polyphagous species are regulated in their preferences chiefly by the presence or absence of taste substances which are presumably non-specific. The physiology of these factors has been discussed in detail by Dethier (1947, 1953).

In short, the physiological mechanism of active selection depends largely upon olfactory and contact chemical (gustatory) stimulation by compounds which are effective at extraordinarily low concentrations. For monophagous and oligophagous species these are chemically specific stimuli which rigidly control feeding. Polyphagous species, which usually feed on any material that lacks repellents, are not held under tight rein by specific compounds, but the differential attractiveness of various acceptable nonrepellent plants undoubtedly owes its being to different, rather labile taste preferences (cf. Brues, 1947, p. 120).

The remaining link in the chain of events consummated by feeding lies in the realm of plant physiology and biochemistry. The plant, which is the source of the chemical stimuli, is by no means a standard repository of specific compounds. It is an extremely complicated organism in its own right. Among its constituents which are of importance from the insects' point of view are chiefly: carbohydrates, fats, proteins, minerals, alkaloids, and essential oils. The last two mentioned comprise those groups that contribute the majority of odors and tastes. The essential oils include benzene derivatives, straight chain compounds, and terpenes. The first two groups are believed to be derived from fat and carbohydrate metabolism respectively. As for the terpenes, available evidence suggests that they are derived from a common precursor in a stepwise fashion (Guenther, 1948, 1949).

It has been shown that these plant constituents vary with the time of day, the seasons, the growth stage of the plant, the tissue, climatic conditions, and soil conditions. Consequently, the plant species or variety, although a botanic entity, is not a chemical entity. It is not homogenous. Rather is it a heterogeneous microchemical environment changing in time and space with changing conditions of growth, climate, and soil. A realization of this situation renders understandable many of the reactions of insects toward their host plants. It is common knowledge that insects oviposit only on certain organs or tissues, that trophic forms will eat certain parts to the exclusion of others, that new growth is frequently preferred to older

tissue, that the plant may be relatively immune from attack at certain seasons, that the same plant variety grown in different geographical areas may be attacked to different degrees, that individual plants in a stand may appear more resistant than others, and that susceptibility may vary with soil conditions.

Of especial importance is the knowledge that the synthetic activity of plants and the composition of their oils is greatly altered by hybridization and polyploidy, and that mutations can interrupt the stepwise production of terpenes at any point (Guenther, 1948). Changes of this nature, occurring in the evolution of plants, act directly upon the insects and are of profound significance in molding feeding preferences. The consequence of these interactions will be realized below.

III

In attempting to solve the riddles of the evolutionary history of active preferences we are inquiring into the emergence of definitive behavior patterns which develop in insects in conjunction with an evolving stimulus field provided by plants. Many stimuli are precepted by the sense organs, but only certain ones have meaning and set off or release an aspect of feeding response. The action of releasing or of token stimuli is believed to be innate (Tinbergen, 1951), that is, the nature of the response is instinctive and its basis genetic. Its survival value depends upon the closeness with which it fits the need to be filled. How have the instinctive responses to diverse token stimuli been evolved?

Since the pattern of insects' feeding habits is by no means static, the progress of evolution can be studied profitably by reconstructing the past from the current phylogenetic picture and by examining carefully contemporary changes and fluxes in feeding preferences. Phytophagous insects were undoubtedly originally polyphagous (Brues, 1920, 1946; Hering, 1926; Takahashi, 1938). Certainly the polyphagous state is more widespread among the older groups although not confined to them. Furthermore, under duress the majority of species are driven to greater polyphagy. Environmental situations which released the feeding behaviour of primitive polyphagous insects were probably very general and non-specific. This conception is certainly in accord with the behavior of contemporary counterparts. Insects are obliged to learn which among a great variety of objects are edible. Two processes, according to Thorpe (1950), may expedite the accomplishment: (1) associative learning on a trial and error principle and (2) habituation. The latter has been defined as "an activity of the central nervous system whereby innate responses to certain relatively simple stimuli, especially those of potential value . . . wane as the stimuli continue for a long period without unfavorable results." Habituation could not operate in monophagous and oligophagous insects but may have been influential in the development of them. If, as Thorpe (*loc. cit.*) states, "learning involved in perception must . . . be phylogenetically prior to anything which could be classed as instinct and must indeed be an essential component, on the perceptory side at least, of even the most rigid instinct," then it is not difficult to conceive how the instinctive behavior characteristic of monophagy and oligophagy might have arisen from a more generalized behavior associated with polyphagy. We can imagine the change as having been brought about through the agency of passive selection aided by associative learning, habituation, natural selection, and isolation, a collective process culminating either in well developed innate preferences or perpetuated phenotypic preferences. Five lines of development from a primitive polyphagous state may be postulated (fig. 1).

(1) Even in the most liberally polyphagous forms as, for example, grasshoppers (Brunsen and Painter, 1938; Pfadt, 1949) and the gipsy moth (Mosher, 1915) the phenomenon of passive selection is wide-

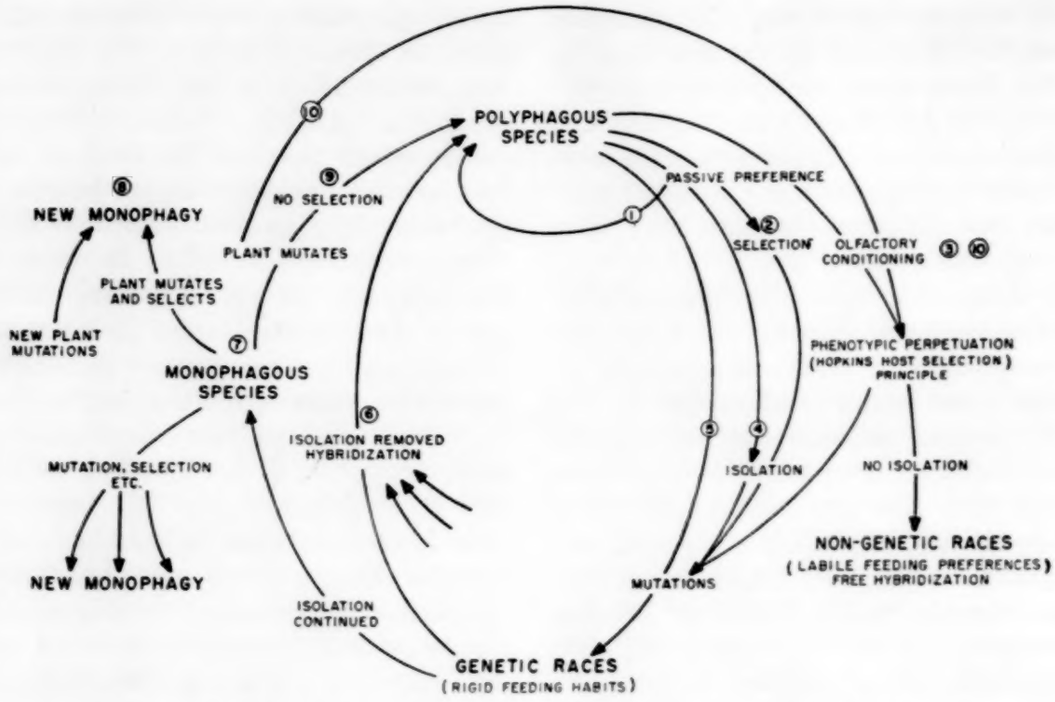

FIG. 1. Postulated lines of development of monophagy and oligophagy from a primitive polyphagous state.

spread. For many species of insects it may be of minor importance only, serving merely to channel the activities of the species into restricted ecological niches or geographical areas or forcing population movements of greater or less magnitude. Caution should be exercised, however, in relating periodic migrations causally to feeding requirements (Williams, 1930). Where the impact of passive selection is slight or transient, the action leads to no significant change in feeding behavior; and the polyphagous habits of a species are retained. Plant-feeding orthopteroid insects represent examples of groups which apparently have retained polyphagy unchanged for a long period of time (Brues, 1920) and are still affected by a type of passive selection.

(2) Types of passive selection exemplified by antibiosis and passive resistance (see p. 39) can, under favorable conditions, form the basis for the establishment of new feeding habits by introducing a selective factor. Of a population of polyphagous insects which settled by chance upon an unfavorable plant, only a small proportion would survive. If the survivors were then isolated by such events as prolonged immature stages, enforced hibernation, reduced activity, or comparable alterations in growth and development which would prevent them spatially or temporally from mating with others of the species, the stage would be set for the development of a so-called resistant race. It is reasonable to imagine the genotype of many polyphagous species as being constituted of large stabilized gene complexes from which special strains characterized by a different frequency of genes may be selected. Spatial isolation would then prevent the mixing of the genes of such strains with those of other segments of the population. It would foster inbreeding. Thus, from a single polyphagous population it ought to be possible to separate groups characterized by dissimilar feeding habits. Indeed, such groups have appeared in nature as resistant varieties of plants have been introduced or developed. Resistant strains exist in polyphagous insects and in those of more restricted feeding habits as well and merely await selection. Painter (1930, 1941) and Painter and Jones

(1948) have shown, for example, that the hessian fly (*Phytophaga destructor*) population of Kansas has consisted of a number of strains which have been selected in the manner indicated above. Similarly, by selection on a laboratory scale it is a simple matter to produce artificially strains of a polyphagous species which will feed successfully on a plant which was, in large measure, unacceptable to the original population. Representative experiments include: transference of the chrysomelid beetle *Phratora vitellinae* from *Salix fragilis* to *S. viminalis* (Schroder, 1903); the scale *Lecanium robinarium* from peach to locust (Marchal, 1908); the caterpillar *Lasiocampa quercus* from oak to pine (Pictet, 1911); the sawfly *Pontania salicis* from *Salix andersoniana* to *S. rubra* (Harrison, 1927). The shifts were attended wtih high mortality rates, and survivors tended at first to be puny. Eventually, however, a normally vigorous population was built up over a period of several generations. Most of the time pioneer feeders experienced as great difficulty in returning to their ancestral plant as they did in adapting to the new one. This fact, plus the initial high mortality, indicates very clearly that a selective process was in progress, and that it screened out from a heterozygous population those forms with changed feeding habits. While selection seems both logical and adequate, it must be admitted that no genetic work has been undertaken to confirm this. Furthermore, accurate information regarding individual variation in host preferences among insects and the variability within polyphagous populations is completely lacking. Careful studies of feeding habit variability among populations of monophagous, oligophagous, and polyphagous species of insects would be invaluable.

There are on record several experiments involving food transference where selection does not suffice to explain the results. Most noteworthy are those conducted with the parthenogenetic stick insect *Dixippus morosus* (Sladden, 1934, 1935; Sladden and Hewer, 1938). Insects were reared on privet, the normal food, for every generation, but samples of each generation were tested for their ability to accept ivy by presentation and preference tests. Only a poor ability to eat ivy was developed. Ivy-bred insects, on the other hand, developed an increased preference for ivy with each successive generation. There was no mortality to be considered, and it would appear that selection was definitely ruled out. The most satisfactory explanation of these results invokes the mechanism of olfactory conditioning, which will be discussed below. For further discussion of Sladden's experiments the works of Thorpe (1940) and Huxley (1942) should be consulted.

All insects cannot be manipulated with equal facility, nor can any and every type of food shift be undertaken. Such diversity indicates that the degree of plasticity varies greatly from one species to the next. Generally speaking, the more restricted a species is in its feeding, the greater the difficulty in altering its feeding habits.

(3) Olfactory conditioning affords another opportunity for the development of altered feeding preferences. From the time of Walsh's (1864, 1865) pioneer discoveries of biological races, the idea has persisted that some sort of memory of larval feeding habits predisposes adults of a polyphagous species to oviposit on the same species of plant as that upon which they themselves had fed. This idea was later enunciated as the Hopkins Host Selection Principle (Hopkins, 1917). Since Hopkins' time numerous investigations aimed at testing the hypothesis have been undertaken. At first glance the collective results appear contradictory. In summary, it may be stated that the principle is valid for some species of insects and not for others (consult Thorpe, 1930 for a list of those which do show a preference for the plant upon which they matured). No evidence favoring the principle was obtained for: the pea weevil, *Bruchus quadrimaculatus* (Larson, 1927); the codling moth, *Carpocapsa pomonella*, which

feeds usually on apples but not infrequently on walnuts (Quayle, 1926); the hymenopterous parasite *Trichogramma*, groups of which were raised on different hosts for as many as 43 to 63 generations (Salt, 1935); the European corn borer, *Pyrausta nubilalis* (Thompson and Parker, 1928). *Artemisia* was believed to have been the original host plant for the corn borer; yet there is no striking ovipositional preference for it. Maize is the preferred plant, both for the *Artemisia* strain and the maize strain; but *Artemisia* exerts a weak attraction for females of its strain while failing to attract those of the maize strain. To this extent the Hopkins Host Principle applies. There is no reason *a priori* to expect identical conditions to exist in different species. The ermine moth, *Hyponomeuta cognatella*, although closely related to *H. padella*, which shows a pronounced tendency to split into biological races, is itself quite stable (Thorpe, 1929, 1931).

Until the demonstration of olfactory and pre-imaginal conditioning by Thorpe and Jones (1937) (see also Thorpe, 1938), there was no sound physiological basis which would satisfactorily explain the principle. Thorpe, and later Cushing (1941), were able to show that certain insects, while in the larval or pupal stages, became conditioned to the specific odors of their host or host plant. The parasite *Habrobracon* can be conditioned to such an extent in the larval stage to the odor of an abnormal host that it will show an ovipositional preference for that host; *Drosophila* can even be conditioned in the larval stage to the odor of peppermint (Thorpe, 1938). While these preferences arising from conditioning are in no wise so strongly ingrained or permanently fixed as any germinal preferences that may exist, they may possibly be adequate to serve in establishing non-genetic races characterized by the possession of specific feeding preferences. Cushing (1944) has presented evidence that the learning of specific feeding habits by the young of certain raptorial birds results in passing on from generation to generation a feeding "tradition." In this way non-genetic feeding races are perpetuated.

The crucial problem is whether a phenomenon like olfactory conditioning can bring about sympatric splitting of a single population into two non-breeding populations. Mayr (1947) has discussed this problem critically in considerable detail. It is clear that in the absence of effective isolating mechanisms there would be free hybridization between individuals with different feeding preferences so that the preferences fostered by olfactory conditioning could never become sorted out genetically. Instead they would at most be perpetuated (because of the female's preference) as "phenotypic races." Thus, in evaluating the significance of olfactory conditioning as an effective factor for the establishment of populations with new feeding preferences, a question of fundamental importance arises, i.e., whether olfactory conditioning by itself can lead to any kind of isolation and bring about a non-genetic mating preference or restriction (cf. Thorpe, 1943, 1944), or whether the isolation must be interjected from another quarter. If, associated with olfactory conditioning, there were also specific mating preferences for members similarly conditioned, that behavior would supply the necessary isolating factor. This, however, is a point upon which few experimental data are available. Where selective mating has been put to test, the results have been positive though not always convincingly so (Thorpe, 1930). Of tremendous import is the knowledge of whether selective mating, when present, occurs in races that are genetic or phenotypic. Again, the genetics of the cases studied are in doubt. The apple-feeding and hawthorn-feeding strains of *Hyponomeuta padella* do exhibit selective mating (Thorpe, 1929). Yet many good species with distinctive feeding habits do not show selective mating and do hybridize freely, as, for example, *Colias eurytheme* and *C. philodice* (Hovanitz, 1948, 1949a, 1949b). Two strains of *Pyrausta nu-*

bilalis, the European corn borer, do exhibit mating preferences for members of their own strain, but here it is known that the strains are fixed on a germinal basis (Arbuthnot, 1944). If it should develop that the preferences exist only in genetic races, then other isolating mechanisms would have to be invoked.

Olfactory conditioning could lead indirectly to isolation through factors other than preferential mating. For example, it is conceivable that the rates of development on different plants might vary sufficiently to isolate adults temporally, that changes in distribution of the plants might effect it, that there might be selective factors, quite apart from the plants themselves, in the respective environments. Or, in the case of an insect whose sphere of activity is restricted to the host or its immediate vicinity, there would be some degree of spatial isolation. Any of these factors, arising as an indirect consequence of restricted feeding, would tend to prevent hybridization. Isolation arising from this or any other origin would enhance the chances of the new feeding habits becoming germinally fixed, but it must be emphasized that the proven existence of isolating mechanisms other than spatial, especially the preferential mating of phenotypic races, is at the moment lacking. Furthermore, there are active forces working against the establishment of sympatric groups isolated by feeding preference alone. One of these is the tendency of animals to pass through a dispersal stage in which they would come into contact with other segments of the population. Another is the reversibility of all conditioning that is not reenforced. The review of Mayr (1947) should be consulted for further details.

The feeding habits of phenotypic races would be expected to be rather labile. Furthermore, it would be expected that under stress of adverse circumstances or changed geographic extension of either the plant or the insect there would be a facile reversion to other feeding habits. In any event, the establishment of phenotypic races would never, in the absence of spatial isolation, lead to genetically determined preferences. With spatial isolation it can be the first step in evolutionary divergence through the operation of the Baldwin-Lloyd Morgan Principle of organic selection. This states, in effect, that modifications repeated for a number of generations may hold a strain within an environment where mutations tending in the same direction will be selected.

(4) Passive selection might operate directly as an isolating factor so as to aid in the establishment of specialized feeding habits. A polyphagous species, by virtue of its catholicity of feeding, is frequently able to occupy widely divergent ecological niches and geographical ranges. Different segments of the population could become restricted to special groups of plants merely by extending their range into areas where one species of plant happens to grow abundantly to the virtual exclusion of others. Or, discontinuities in plant ranges arranged so that one segment of the insect population found itself in a different plant community from the other, and isolated, would assist in the differentiation of distinct gene frequencies in the two segments of the population. Plant diseases, fire, increasing xeric conditions, inundation, normal plant succession, glaciation, and cultivation in recent times, all may be operative at one time or another.

Very few examples of direct isolation are well documented, but two, based on indirect evidence, may be given as illustrative. Larvae of the geometrid moth *Oporabia autumnata* feed in Europe on *Betula, Alnus, Larix,* and *Pinus*. The subspecies *filigrammaria* feeds in the larval stage on *Calluna, Erica,* and *Vaccinium*. Harrison (1920) believed that *filigrammaria* evolved from *autumnata* with the assistance of climax glaciation which isolated the parent species into two groups, one in the southeast of Europe and the other to the west of Great Britain. It was presumed that conditions in the west favored

the growth of *Calluna* and related species to an extent which caused a reduction in the ancestral plants, *Betula,* etc. Consequently, one group of moths was restricted to feeding on Ericaceae while the other remained on the original food plants. At the present time *filigrammaria* larvae prefer *Calluna* and other ericaceous plants but retain the ability to eat and develop on birch as evidenced by successful breeding for five generations. Conversely, *autumnata* feeds successfully on *Calluna.* Within historical times a larch feeding race of the *Betula-Alnus*-feeding species has developed as a result of isolation following the replacement of alders by plantings of larch. Unfortunately, tests were not conducted to determine whether the races so developed are now genotypic or phenotypic. Nevertheless, the example illustrates one way in which a population may be split by the discontinuities and vagaries of plant distribution.

A rather similar account is given of race evolution with concomitant feeding preference development in the silkworm moth genus *Platysamia* (Sweadner, 1937). At the beginning of the ice age in North America *Platysamia* stock was presumed isolated in two groups, one in the southeast and the other in the southwest. From the former the present species *P. cecropia* arose; from the latter, the species *P. euryalis* and *P. gloveri.* The factor which isolated the two groups was considered to have been the presence of treeless plains since the larvae are restricted in their feeding to deciduous trees and shrubs. *P. cecropia* is liberally polyphagous in its habits; *P. gloveri* feeds on *Salix, Ribes,* and *Alnus.* As the ice retreated and the trees followed, the moths extended their respective ranges north. Hybridization of *P. gloveri* and *P. euryalis* in the region of Nevada gave rise to the form *P. kasloensis.* When forms migrating up the Rocky Mountain chain reached Canada, there appeared a bridge to the eastern forests in the form of the wolf willow *Elaeagnus.* Part of the genus became adapted to this food plant and to *Salix* and gave rise to the species *P. nokomis.* Once established in the east *P. nokomis* is supposed to have split into two groups one of which became adapted to larch and gave rise to *P. columbia.* Today the form *P. nokomis* feeds primarily upon *Elaeagnus* and *Salix;* the species *P. columbia,* on *Larix americana.*

(5) The evolution of restricted feeders from polyphagous forms has been postulated as arising directly by mutations which subsequently became reproductively isolated from the parent stock. It is difficult to imagine how this end could be achieved in practice. In general, the importance of genetic changes as primary isolating mechanisms is seriously questioned (cf. Dobzhansky, 1941; Huxley, 1942; Mayr, 1942). Specifically, the problem of isolating mutants with restricted preferences from a parent polyphagous stock does not appear possible especially since the polyphagous stock could equally well feed on the plant preferred by the mutant.

There remain for discussion the histories of the aphids, leaf hoppers, leaf miners, and gall wasps, groups about which an enormous volume of unrelated facts relating to feeding have accumulated, but in each case the lack of key experimental data makes any detailed interpretation of the evolution of their feeding preferences in terms of modern concepts hazardous. It also seems wise to hold in abeyance new discussions of the intriguing problem of host alternation (see Mordwilko, 1928; Kennedy and Booth, 1951). The gall wasp (*Cynips*) story is only slightly more amenable to analysis. This genus, which is restricted to white oaks, is presumed to have originated in the southwestern North America during the Oligocene or Miocene. Oaks are believed to have originated in the identical area and era. It is assumed that *Cynips* was always associated with oak. The Pacific coast population *Besbicus* is restricted to the group of oaks centering around *Quercus lobata, Q. dumosa,* and *Q. garryana.* It is thought to have reached the

Sierras before the Great Basin became arid in the Miocene. Ancestral stocks of *Cynips echinus* and *C. guadaloupensis* are said to have perpetuated a preference for *Q. lobata-dumosa* and *Q. chrysolepsis* respectively. *C. centricola* is restricted to *Q. stellata*. The *C. mellea* group shows a preference for *Q. stellata;* the *C. pezomachoides* group for the *Q. alba* group; the *C. gemmula* group for the *Q. prinus* group. Kinsey (1936) believed that speciation in *Cynips* arose most commonly by mutation and hybridization followed by isolation in which strict host preferences played an important role (but cf. Dobzhansky, 1941). The lack of physiological and ecological experiments designed specifically to elucidate the mechanism of host plant selection coupled with the absence of pertinent biochemical studies on the oaks, which are a heterogenic group including a great number of biotypes (Chaney, 1949), are obstacles to further analysis.

If genetic races characterized by different feeding preferences could have become established, thereafter the usual mechanisms of isolation and selection would work toward speciation. Usually, spatial isolation operates first. This goal, the origin of new species, is related to the present discussion only insofar as the establishment of a species might signal the achievement of a new fixed feeding behavior. The question of the actual existence of genetically established feeding races has not been sufficiently well investigated to indicate the frequency of these groups in nature. In very many cases crucial experiments which would identify genetic and phenotypic races have never been undertaken. Some pertinent data are available for eight groups, but no clear picture emerges from these. There is little doubt that preferences in strict monophagous and oligophagous species are germinally fixed. The extent to which genetic and acquired preferences intergrade in polyphagous species and various races remains untested. Denso (1909) crossed the two hawk moths, *Pergesa elpenor* ♂ which feeds on *Epilobium* and *Celerio hippophaes* ♀ which feeds on *Hippophae rhamnoides*. The gravid females naturally laid their eggs on *H. rhamnoides*, but the larvae would feed only on *Epilobium*. *Harrison* (1926), working with geometrid moths, crossed males of *Lycia hirtaria*, which feed on many species of deciduous trees and shrubs, and females of *Nyssia graecaria* and *N. zonaria*, which feed on *Achillea millefolium*, and other low-growing herbaceous plants. Hybrid larvae fed only upon the food of the male parent. They were sterile, so further crosses could not be made. Since hybrids of *Poecilopsis pomonaria*, which feeds on many deciduous trees and shrubs, including *Crataegus*, and *P. isabellae*, which feeds solely on larch, are cross-fertile, more extensive studies could be undertaken with these species. F_1 larvae from reciprocal crosses fed solely on larch. All other crosses and back crosses up to the F_4 produced only larvae which would feed exclusively on hawthorn. This reported result is difficult to explain on any genetic basis. Sweadner's (1937) experiments on hybridization in the genus *Platysamia* yielded no information of pertinence here because all hybrids fed successfully on *Prunus serotina*. Two subspecies of the moth *Celerio, C. euphorbiae* and *C. mauretanica* normally feed on *Euphorbia* and refuse *Salix*. Yet the hybrid from *C. euphorbiae* ♀ × *C. mauretanica* ♂ and from the reciprocal cross fed readily on *Salix* (Goeschen, 1913; cf. also Schulze, 1913). Hybridization experiments in the butterfly genus *Basilarchia* by Edwards (1877) and Field (1910, 1914) yielded little information of value, again because the feeding habits of the several species are rather labile. Two species are concerned, *B. astyanax* and *B. arthemis*. The hybrid of these two is the form *B. proserpina*. Larvae from a cross between *B. astyanax* ♀ and *B. arthemis* ♂ fed only on cherry, the food plant preferred by *B. astyanax*. A captured female *B. proserpina*, oviposited only on *Prunus serotina* the preferred plant of

B. astyanax and refused birch, poplar, and willow, the preferred plants of *B. arthemis*. Larvae from the eggs laid by this female fed on *Prunus* and metamorphosed into adults of which nine were *B. proserpina* and seven were white banded *B. arthemis*. Larvae from a cross between *B. archippus* ♀ and *B. arthemis* ♂ fed on willow, a food plant acceptable to both parents. These larvae developed into typical *B. proserpina*. Inability to extend the experiments to succeeding generations precluded a thorough analysis of the genetics of the feeding preference. Hovanitz (1944), working with *Colias* butterflies, has shown that *C. eurytheme* is sterile if the larvae are reared on red clover; *C. philodice*, sterile if the larvae are reared on alfalfa. In neither case, however, do the adults exhibit oviposition preferences, nor the larvae, feeding preferences. The different diet requirements of the two species, and phenotypic alterations, as well as the presence or absence of diapause, have a genetic basis which is multifactorial.

Two different strains of the European corn borer, *Pyrausta nubilalis*, were introduced into the United States. The one in New England is a multivoltine strain; i.e., it produces more than one generation per year. The mid-western strain was originally univoltine. It has been shown by Arbuthnot (1944) that the eastern strain is homozygous multivoltine; the Toledo strain, a mixture of univoltine and multivoltine generations. A strain of homozygous univoltine moths could be isolated from the latter, but no homozygous multivoltine moths could be produced. Evidence indicated that the univoltine state is recessive. There is a clear indication of a difference in host plant relationships in the two strains (Painter, 1951). The New England multivoltine population feeds upon 200 different plants; the midwestern strain is more rigidly restricted to corn and a few weedy plants associated with corn. Moths of the two strains exhibit distinct mating preferences for members of their own strain.

Once races have become firmly established they would tend to maintain their identity by one or more of the several mechanisms of isolation. Should these be discontinued, the course is open for free hybridization with other races to occur. By such a process secondary polyphagy can arise. This has undoubtedly occurred quite frequently in evolution. On the other hand, effective isolation, now reinforced by association with special plants and ecological niches would lead to the development of species with narrowly restricted feeding habits. These in turn by direct mutation might give rise to forms with aberrant feeding habits, and, if spatially or reproductively isolated, would represent the genesis of races within a species separated solely by feeding preferences. In the last case the problem is again that of separating the mutants from the parent stock so that geneflow is prevented. Mayr (1947) has pointed out that new mutants in diploid bisexual animals always occur first as heterozygotes which will form a bridge with individuals in the parent stock. A possible mechanism whereby a shift of feeding habits might occur was suggested by Stern (see Mayr, 1947):

"Let the animal *AA*, which is host specific on plant 1, have the mutation *a* which in homozygous condition produces host specificity for plant 2. Let us then make the following assumptions:

"Assumption 1: Let *AA* live only on plant 1.

"Assumption 2: Let *aa* live only on plant 2.

"Assumption 3: Let the heterozygotes *Aa* be exactly like *AA*.

"Assumption 4: Let there be little or no dispersal in the reproductive phase so that *A* animals do not meet *aa* animals.

"Assumption 5: Let *A* be ill adapted to plant 2.

"Assumption 6: Let *aa* be ill adapted to plant 1.

"Assumption 7: Let segregated *aa* formed on plant 1 have difficulties in finding plant 2, even though the original *aa* found 2.

"Then there will be little mixing between the populations on 1 and 2 and the opportunity is provided for a gradual piling up of additional genetic differences between these populations."

Whether or not such a scheme can work remains to be seen. All evidence favoring the origin of new restricted feeding habits is at best indirect and poorly documented. Food plant changes in the pierid butterflies constitute one case. Pierid larvae are essentially cruciferae-feeders, but a few genera attack the Leguminosae. Members of the genera *Catopsilia* and *Callidryas* are restricted to the single plant genus *Cassia* in widely separated parts of the world. It has been proposed (Brues, 1924) that the acquisition of a leguminous food plant arose as the result of a mutation or some equally basic change.

Within historical time a change which can best be explained on the basis of mutations has occurred in the feeding habits of the apple-maggot fly, *Rhagoletis pomonella*. The apple-maggot fly appears to be native to North America, where it apparently bred originally in *Crataegus*. At the present time there are two strains, one of which breeds in blueberries and the other in apples. In the state of Maine the blueberry strain has been present from earliest historical times; the apple form originated within very recent times. Attempts to transfer the apple strains to blueberry and vice versa have been entirely unsuccessful (Woods, 1915).

Up to this point all postulates imply changes and mutations largely on the part of the insect against a rather stable or ineffective plant background. This idea, of course, hardly represents an accurate description of events. The plant undergoes evolution and exerts a selective effect on both polyphagous (fig. 1, stage 2) and monophagous insects (7–10). Consequently, feeding preferences may change to accommodate plant changes, and monophagous insects as well as polyphagous ones enlarge their menu to include additional plant species as convergent plant evolution progresses (8). The scheme of evolution of feeding preferences in the butterfly genus *Papilio* proposed by Dethier (1941) is a case in point. It illustrates a sequence by which an insect may be brought into contact with new odors to which it can become conditioned, and thus, by incorporating additional botanical units into its life, become exposed to new streams of genetic change.

The four hundred or so species in the genus *Papilio* may be grouped into four categories: (1) species whose feeding habits are varied; (2) *Aristolochia*-feeders; (3) Umbelliferae-feeders; and (4) Rutaceae-feeders. Investigation into the feeding habits of the latter two groups reveals some suggestive trends in the evolution of feeding habits in that section of the genus.

Only eleven species of *Papilio* are now known to eat Umbelliferae. These are: *P. ajax* and its races, *P. bairdi* and its races, *P. zelicaon*, *P. indra*, *P. machaon* and its races, *P. hospiton*, *P. alexanor*, *P. demoleus*, *P. ophidecephalus*, *P. constantinus*, and *P. paeon*. It is curious that in a large cosmopolitan group with more or less standard feeding habits a few species should have acquired the Umbelliferae-feeding habit. The fact that Umbelliferae-feeders as exemplified by *P. ajax* will eat species of *Ruta* suggests that they probably formerly belonged to the Rutaceae-feeders. To understand the transition from Rutaceae-feeders to Umbelliferae-feeders, it is necessary first to consider the changes that have taken place in Rutaceae-feeders. Rutaceous plants may be divided on the basis of their essential oils into four groups: those with lemon or orange-like odor containing citral (e.g. *Citrus*), those with a rue odor containing methylnonylketone (e.g. *Ruta*), those containing both oils in varying proportions (e.g. *Zanthoxylum*), and those of a mint

or camphor type. Most of the evidence points toward species of *Citrus* as being the original host plants of Rutaceae-feeders. The transition of *Citrus*-feeders to *Ruta*-feeders may have been gradual, that is, *Citrus* to *Zanthoxylum* to *Ruta*. Then the transition from Rutaceae-feeders to Umbelliferae-feeders may have been affected by means of the rutaceous plant *Dictamnus fraxinella,* which contains methyl chavicol and anethole (compounds found in Umbelliferae), or *Pelea madagascarica,* which contains anethole. It seems probable, however, that the change to such plants as *D. fraxinella* and *P. madagascarica* proceeded by way of intermediates, *Zanthoxylum* and *Ruta,* and not directly from *Citrus*. The proposed line of evolution would then be *Citrus* (and plants containing citral) to *Zanthoxylum* (or other plants containing citral and methylnonylketone in varying proportions) to *Ruta* (or plants containing methylnonylketone) to *D. fraxinella* (or similar plants containing methyl chavicol, anethole, etc.). Or *Ruta* may have been omitted from the series. *P. cresphontes,* for example, feeds on a wide variety of Rutaceae of different chemical constitution (Dethier, 1941). Some species such as *P. andraemon, P. cresphontes, P. machaon,* and *P. ajax* represent various steps in the change from one feeding habit to a new and different one. The acceptance of food plants from other families (e.g. *Piper*) may be explained in part by their chemical composition.

In just which direction *P. hospiton* and *P. alexanor* are progressing is difficult to determine in the face of such a paucity of facts. Whether they eat any plants other than species of *Ferula* and *Seseli,* which are characterized by the presence of sulfides, is not known.

As indicated earlier, those characteristics of plants which are operative in host selection, be it active or passive, have a genetic basis. It has been shown that some are due to single genes and others to multiple factors (Painter, 1951). It is even possible that plants which have been exposed to insect attack for the longest periods of time would by natural selection develop resistant factors to a greater degree than others (Painter, *loc. cit.*). In some species preadaptation occurs. A well known instance of the development of resistant strains in the absence of insect attack is that characteristic of sorghum (Snelling *et al.,* 1937; Painter, 1941). Varieties brought to the United States from Africa and Asia, where neither chinch bugs nor similar sorghum pests exist, already exhibted marked resistance to chinch bugs.

As an alternative to the evolving plant acting as a selective screen for those insects which alone can accommodate to a particular plant mutant, there is the possibility of those insects being selected which will accept *all* of the mutants (9). Greater plasticity of this sort would lead to the development of a polyphagous group. Or, if the various plant mutants were to exercise no selective value as far as the insect is concerned, polyphagy would again develop. A similar set of circumstances, that is, no selective action, could and does work in another direction for those insect species which undergo olfactory conditioning (10). From a monophagous species phenotypic races theoretically would arise.

Summary

In viewing the evolution of feeding habits within historical time we observe some insects remaining constant for long periods, some shifting gradually to new plants or enlarging their menu, some altering feeding preferences quite suddenly, some polyphagous species forming biological races, others not, introduced insects attacking plants not previously known to be acceptable, and native insects shifting their attack to introduced plants. These kaleidoscopic patterns of behavior merely reflect the diverse ways in which different insect species may respond to changes within the plant. The drama of changing feeding preferences observed currently and in the past thus

resolves itself into a dynamic equilibrium between two changing systems, the plant and the insect. The outcome at any particular time depends in large measure on the genetic potentialities and relative rates of change and stability in the two organisms.

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STATISTICS AND THE EVOLUTION OF DICOTYLEDONS

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It has become increasingly clear, in the last few decades, that discussions of the course of evolution in groups of organisms which lack a comprehensive fossil record are futile so long as those who hold opposing views base their arguments on preconceived ideas. Nowhere does this apply with greater force than to the evolution of flowering plants, where the fossil record, restricted as it is to post-Jurassic times, gives little or no direct evidence. Under these circumstances, before any further progress can be made, a radical change is essential both in mental approach and in thought processes. In ridding our minds of all personal convictions not founded on scientific evidence, not only must we examine in the minutest detail our basic assumptions, their factual justification and their logical implications whenever our own beliefs differ from those of others, but we must also do so even when there is little or no disagreement. Only then shall we be in a position to build a theoretical structure which is likely to survive. Yet, reading through the works of students of evolution, how seldom it is that the full reasoning is clearly stated. Frequently, it is true, basic assumptions are stated, but not the evidence on which they are based. Thus, in the field of dicotyledon evolution, it is common to find listed a number of trends which are assumed to have occurred, e.g. (Bessey, 1915) from woody habit to herbaceous, from hermaphrodite to unisexual, etc., but one looks in vain for the thought processes lying behind these assumptions. Of the two quoted, the first assumption is almost universally accepted, for there are few who do not agree that, among dicotyledons, the woody habit is primitive. But what real evidence has been put forward in support of this view? All too often in such cases, as Turrill (1942) has emphasised, the evidence can be reduced to a circular argument around primitive characters and primitive organisms. Yet most of the phylogenetic schemes of classification, so far produced, are based on such insecure foundations. The criticism lies not so much with the basic assumptions themselves, for many of them are probably correct, as with the reasons for their acceptance.

It was with such thoughts in mind that a few years ago, (Sporne, 1948 and 1949), I made an attempt to cut the Gordian knot by reducing to mathematical terms the discussion of evolution in large groups of organisms, thereby avoiding, as far as possible, the effects of personal bias. The starting point lay in the generally acceptable view that the process of evolution involves the acquisition of new characters in addition to, or in exchange for, old ones. On this were based a number of definitions, to which no objection has, so far, been made. In addition, there was the hypothesis that trends in evolution have occurred, i.e. that certain changes have taken place in several different lines of evolution. It was then shown that, if such hypothesis be correct, the characters concerned in these trends will exhibit mathematical correlation. Thus, within a particular group of organisms, if two ancestral characters A and B have shown a tendency to evolve into the advanced states A′ and B′, statistical analysis of the whole group should show a positive mathematical correlation between A and B and also one between A′ and B′. (Similarly, there should be negative correlations between A and B′ and between A′ and B.) It is to be emphasised that such correlations are to be expected, whether the group is monophyletic or not, provided

that the trends have taken place within the group as a whole.

Caution is, however, necessary in applying these arguments in reverse, i.e. in concluding that, because a particular pair of characters are correlated, they must necessarily be either primitive or advanced. Correlations between isolated pairs of characters are capable of several other explanations: (1) the two characters may be under the influence of one and the same genetic factor, (2) they may stand in some physiological relationship to one another, (3) they may be biologically interdependent, (4) they may be interdependent by definition alone, e.g. the definition of one character may presuppose the existence of the other. Cases where the last explanation applies should be obvious, but the others are not so simply accounted for, especially if only one pair of characters is under consideration and if they are closely associated in the organism, either in time or in space. They become less and less probable as more and more characters are shown to be correlated. Analysis of the dicotyledons of the world, as classified by Engler and Diels (1936), showed the existence of at least twelve characters which are mathematically correlated when considered in pairs. Among them were some involving vegetative organs, some floral organs and some the seed—organs so widely separated on the plant, either in space or in time, as to render unlikely the suggestion that they are all connected genetically, physiologically or biologically. A few pairs of characters, e.g. zygomorphic corolla and meiomerous androecium, might indeed be intimately concerned in the biological efficiency of the flower, and correlation between them, if isolated from the rest, would be capable of explanation on these grounds, but, when considered in relation to the remaining ten characters, even these floral characters were seen to be indicators of evolutionary advance. This conclusion was confirmed by a statistical comparison of the fossil record with the present-day flora of the world. The primitive dicotyledon was pictured as "a tree or shrub, with alternate, glandular, stipulate leaves, with unisexual, actinomorphic, polypetalous flowers, with many stamens and many carpels, and with arillate seeds whose two integuments were vascularised."

In a recent paper in this journal, Stebbins (1951) has attempted to discredit the arguments leading to these conclusions. Starting with the same hypothesis that "there are certain trends in floral evolution which are repeated many times in groups with very diverse affinities," he considered eight floral characters, for each of which two possible conditions are recognised, one taken to be advanced and the other primitive. In deciding which is the advanced condition in each case, he was content to take generally accepted views as correct, e.g. "the absence of petals, the union of petals and sepals, the union of carpels . . . , the reduction of seeds to one per carpel, and the inferior ovary are all frequently recognised as advanced conditions." He then analysed the occurrence among angiosperms of different combinations of these eight characters and showed that certain combinations are much more frequent than others. These he described as "adaptive peaks," representing the most successful flower types. Then, taking in pairs the supposed advanced condition of these characters, he calculated, by the χ^2 method, their degree of correlation. Discrepancies were shown to occur, in that some correlations were positive and some negative, and these discrepancies were claimed to disprove my contention that advanced (or primitive) characters may be expected to show positive correlation. It is the purpose of the present paper to consider whether this claim is justified.

Two points of difference should be emphasized at the outset. Firstly, the work of Stebbins covered all the angiosperms, whereas mine was restricted to dicotyledons, and secondly, his discussion was limited almost entirely to characters concerned with pollination or seed-dispersal, whereas mine ranged over vegetative as

well as floral characters. The first of these points of difference is probably not important, particularly if the angiosperms are a monophyletic group, or at any rate if similar trends have occurred in both the monocotyledons and the dicotyledons. However, the cautious procedure would have been not to assume this, but to consider first the dicotyledons, then the monocotyledons and only to combine them if analysis of the two separately should justify such action. The second point of difference is, however, much more important, for if discussion is restricted to floral characters, any correlations which may occur are capable of the several explanations outlined above. Stebbins claims that it is the functional association between characters which operates, to the exclusion of their evolutionary status, in bringing about correlations. What is more likely, however, is that both factors operate simultaneously. Under these, circumstances, the first may augment the second or may obscure it. Thus, it might happen that two advanced characters are incompatible, on functional grounds, to such an extent that they show no correlation at all or even a negative one. In this way discrepancies, such as those demonstrated by Stebbins, could arise.

Before enlarging on this, however, there are a number of points in Stebbins' paper which require comment. Several of these arise from the unorthodox use of botanical terms. Thus, "monochlamydeous groups, with the petals absent, were placed in the advanced sympetalous classification if the sepals were united." Taking the definition of sympetaly in this way, Stebbins had no misgivings about a correlation between sympetaly and apetaly. Most botanists would, however, disagree with this use of the term. They would hold that, by definition, sympetaly involves the possession of petals and that any correlation between sympetaly and apetaly is meaningless. Furthermore, all other calculations which involve sympetaly should exclude apetalous families. Similar remarks may be applied, though with less force perhaps, to the definition of zygomorphy —"Flowers were considered zygomorphic primarily on the basis of their corollas, but in some groups, particularly those related to clearly zygomorphic forms, zygomorphy was recorded chiefly on the basis of stamens, particularly if the number of stamens was fewer than that of the corolla lobes." This is unsatisfactory since it requires the introduction of the personal element in deciding as to the correct placing of certain groups. In addition, however, there are many who would wish to restrict the term to the corolla, in which case a correlation between apetaly and zygomorphy would be meaningless; and moreover, apetalous families should be excluded from all other calculations involving zygomorphy.

The correct treatment of placentation raises a number of difficult problems, and Stebbins has not found entirely satisfactory solutions to them. The terms axile and parietal are normally applied to flowers in which several carpels are fused. They have no meaning when applied to apocarpic flowers like those of *Ranunculus* or to monocarpellary flowers like those of *Lathyrus*. Yet Stebbins treats such cases as axile and, naturally therefore, discovers a correlation between syncarpy and parietal placentation. This correlation owes its existence entirely to the mis-application of definitions. Calculations involving placentation should be restricted to syncarpic families. This, however, raises the problem of the correct treatment of unilocular ovaries. Some are clearly the result of the fusion of a number of carpels; others are clearly one single carpel, but there are many families, whose ontogeny has not yet been studied, where the number of carpels is a matter of opinion. It is not even certain whether the carpel is a valid concept of universal application. In our present state of knowledge therefore, placentation is rather an unsatisfactory character for statistical treatment.

The characters which Stebbins used were:—apetaly, sympetaly, zygomorphy, reduced number of stamens, syncarpy,

reduced number of ovules, parietal or basal placentation and epigyny, all of which were taken to represent the advanced condition; the woody habit was also considered for the purpose of comparison with my own findings. Of these, it will be noticed that three characters, besides the woody habit, were also considered by me, viz. fusion of petals, symmetry and number of stamens. With regard to these three characters, Stebbins' findings and mine are in agreement, his being concerned with the advanced condition and mine with the primitive. Further study enables me to add another character to the list of ancestral ones given above, for the type of endosperm shows a high degree of correlation with the other characters, nuclear endosperm being primitive and cellular endosperm advanced. It has also been found that information listed by Metcalfe and Chalk (1950) on the presence of secretory cells is more comprehensive than the list of families with glandular leaves given by Blenk (1884) and should be used in place of it. With these additions and alterations, my list of characters has been combined in Table I with the list of characters used by Stebbins and correlations between all eighteen characters have been re-calculated. The symbols + and − represent positive and negative correlations whose significance is greater than that corresponding to p = 0.02. The symbols + and − indicate differences between the observed and the calculated figures which are not sufficiently great to bring the value of p to 0.02, while ○ represents complete absence of correlation. Squares in which any correlation would be meaningless have been blocked in. In addition, table I shows a compari-

Table I

		1 Woody habit	2 Secretory cells present	3 Leaves alternate	4 Stipules present	5 Flowers unisexual	6 Flowers actinomorphic	7 Petals free	8 Stamens pleiomerous	9 Carpels pleiomerous	10 Seeds arillate	11 Two integuments	12 Integument bundles	13 Nuclear endosperm	14 Carpels free	15 Axile placentation	16 Hypogynous or perigynous	17 Petals absent	18 Seeds few		London Clay	Pre-Pleistocene Wood
Seeds few	18	+	-	-	-	+	○	-	−	−	−	-	·	○	○	+	-	+			·	+
Petals absent	17	·	·	-	○	+			·	-	-	○	-	-	○	−	○				−	○
Hypogynous or perigynous	16	○	○	·	·	○	·	○	○	·	·	+	-	·	·	+					○	-
Axile placentation	15	+	○	○	+	○	·	+	·	+	·	○	·	○							+	○
Carpels free	14	○	·	○	·	·	○	○	+	+	·	+	·	○							·	○
Nuclear endosperm	13	+	+	·	+	·	·	+	+	·	·	+	+								·	·
Integument bundles	12	+	+	·	·	+	○	·	+	·	+	·									+	+
Two integuments	11	+	+	·	+	·	+	+	+	+	+										·	+
Seeds arillate	10	·	·	+	+	·	○	+	+	·											+	·
Carpels pleiomerous	9	+	+	·	+	·	+	+	+												+	·
Stamens pleiomerous	8	+	+	+	+	·	+	+													·	·
Petals free	7	+	+	·	+	·	+														·	·
Flowers actinomorphic	6	+	+	·	·	+															-	·
Flowers unisexual	5	+	·	·	·																+	+
Stipules present	4	·	+	○																	+	+
Leaves alternate	3	+	·																		+	·
Secretory cells present	2	+																			+	+
Woody habit	1																				+	

son of the fossil record with the present-day flora of the world in respect of these eighteen characters, and for this purpose the same two lists were used as in previous papers: (1) that of families occurring in the London Clay flora (Reid and Chandler 1933), (2) that of families whose wood has been identified from pre-Pleistocene deposits (Edwards 1931). As previously emphasised, these lists are not satisfactory as random samples of fossil floras of the world, but at the same time it must be realised that they are used only indirectly in deciding which characters are primitive. What is remarkable is that such an unsatisfactory fossil record exhibits correlations with any of the eighteen characters.

Since the number of significant positive correlations exhibited by any particular character is a measure of its reliability as an indicator of evolutionary advancement, it is clear from Table I that some characters are much less reliable than others. Several reasons for this may be suggested. The first, of which a hint has already been given, is that certain pairs of advanced characters may be incompatible, in that they tend not to occur together in one and the same flower, such incompatibility being sufficient to nullify any positive correlation or even to convert it into a negative one. Other possible reasons for the unreliability of certain characters may be inherent in the methods used for analysing the data, as for example, in deciding on the correct treatment of rare occurrences of the particular character. Thus, it may occur in only one species out of several hundred constituting a large family and in only one species out of five constituting a small family. The problem then arises as to whether these two families should be treated in the same way or not. To suggest taking the genus, instead of the family, as the statistical unit would only be a partial solution to the problem, for there are both large and small genera, just as there are large and small families, and in any case, the magnitude of the task would make it impossible.

Characters 1 to 15 are more reliable than the remaining three, for of the 104 possible correlations between them, 54 are highly significant and positive, 37 are less significant and positive, while there are no negative correlations at all. This evidence, alone, indicates that these fifteen characters are all primitive or all advanced. Evidence from the fossil record confirms that they are primitive. Concerning "hypogyny or perigyny" (character 16) the evidence is rather less conclusive, for of the possible correlations with the previous fifteen, although there are no highly significant negative ones, there are only two which are highly significant and positive. Thus, although there is little doubt that this character is primitive, the evidence does not establish it with absolute certainty. Regarding "apetaly" and "small number of seeds" (characters 17 and 18 respectively), the evidence appears actually to be conflicting, for there are some highly significant negative correlations as well as positive ones. These inconsistencies are not peculiar to dicotyledons, for Stebbins found similar inconsistencies in the angiosperms as a whole. They are not sufficient, however, to invalidate the thesis that primitive (or advanced) characters are correlated with one another. All that they do suggest is that apetaly and small number of seeds are not reliable indicators of advancement. Two possible explanations have already been given, but there is also a third, which has not been mentioned so far and which seems to be particularly applicable to these two cases. The suggestion is that these two characters may ocur, as ancestral characters, in very primitive families and, by secondary processes of reduction, in some very advanced families. Under these circumstances, conflicting correlations might well be expected. So far as these two characters are concerned, Stebbins assumed them both to be advanced. The evidence for regarding a large number of seeds as primitive, how-

ever, is derived chiefly from anatomical work on restricted groups of flowering plants and, whereas the arguments may apply within these restricted groups, they do not necessarily apply to angiosperms as a whole. Number of seeds should not be considered separately from size of seeds. Stebbins is aware of this, for he pointed out that, on mechanical grounds alone, large seeds necessarily are limited in numbers, but he made no reference to the suggestion put forward by Corner (1949) that the large seed is primitive. If this suggestion is corect, however, it follows that a limited number of seeds is likely to be primitive, where the seeds are bulky, even though it may be advanced where the seeds are relatively small. Similarly, apetaly could have been the ancestral condition in flowering plants (better described as haplochlamydy in this case) and could have re-appeared by the loss of petals in some advanced families. Similar considerations also apply to the unisexual flower, even though this is not apparent from table I, for, whereas the evidence of correlations proves it to be an ancestral character, it is clearly at times a derived condition (particularly when rudiments of the opposite sex are present). The extraordinarily high degree of correlation between unisexuality and haplochlamydy, already referred to (Sporne, 1949), now acquires enhanced interest. Three factors contribute to it, for not only are the two characters associated on functional grounds, as shown by Stebbins, but they occur together in primitive families and also in some advanced families. Which particular interpretation to apply in each example of apetaly can only be an arbitrary decision, in our present state of knowledge, and the same applies to unisexuality in flowers which lack rudiments of the opposite sex. These characters should, therefore, be used only with great caution in assessing advancement. Seed number is open to the same objections in its interpretation and should be used warily. Seed size might, perhaps, prove more useful than seed number, but there would still be some need for arbitrary decisions, for it is not clear whether absolute size is the correct criterion or whether it should be size of seed relative to size of the whole plant.

It is apparent that these cautionary remarks apply with greater force to discussions of advanced families than to discussions of primitive ones. So, while there is some justification for including characters 5, 16, 17, and 18, when deciding which families of dicotyledons approach most nearly to the ancestral type, it is better to omit them when treating the dicotyledons as a whole. As explained in previous papers, it is possible to arrange the families of dicotyledons roughly in order of their advancement by calculating an "advancement index," and this has been done, using the fourteen characters whose reliability is not in serious doubt. The most primitive are those families whose advancement index is nearest to zero and the most advanced are those with an index of 100.

Advancement Index %	
14	Magnoliaceae.
15	Bombacaceae, Flacourtiaceae.
18	Anonaceae, Leguminosae, Malvaceae, Myristicaceae.
21	Rhizophoraceae.
25	Crossosomataceae, Dipterocarpaceae, Euphorbiaceae, Myrtaceae, Sapindaceae, Tiliaceae, Trochodendraceae.
27	Himantandraceae.
29	Lecythidaceae, Ochnaceae, Rhamnaceae, Rosaceae, Sterculiaceae.
31	Bixaceae, Caryocaraceae, Chlaenaceae, Dilleniaceae, Elaeocarpaceae, Eucryphiaceae.
32	Guttiferae, Nymphaeaceae, Platanaceae.
33	Akaniaceae, Eupomatiaceae, Fagaceae, Lactoridaceae.
35	Cunoniaceae, Phytolaccaceae, Quiinaceae.
36	Aizoaceae, Resedaceae, Salicaceae, Theaceae, Thymelaeaceae, Vitaceae.

Advancement Index %	
38	Aristolochiaceae, Calycanthaceae, Connaraceae, Didieraceae, Marcgraviaceae, Stachyuraceae.
39	Anacardiaceae, Celastraceae, Cochlospermaceae, Ebenaceae, Erythroxylaceae, Meliaceae, Ranunculaceae, Staphyleaceae.
41	Monimiaceae.
42	Berberidaceae, Betulaceae, Buxaceae, Cercidiphyllaceae, Lardizabalaceae, Medusagynaceae, Nepenthaceae, Sonneratiaceae, Ulmaceae.
43	Cneoraceae, Melastomataceae, Papaveraceae, Simarubaceae.
44	Leitneriaceae.
45	Achatocarpaceae, Gyrostemonaceae, Hernandiaceae, Myricaceae, Urticaceae.
46	Begoniaceae, Combretaceae, Elatinaceae, Hamamelidaceae, Hippocrateaceae, Lauraceae, Melianthaceae, Menispermaceae, Oxalidaceae, Pentaphylacaceae, Portulacaceae, Sapotaceae, Tamaricaceae, Tremandraceae, Violaceae.
50	Brunelliaceae, Cactaceae, Canellaceae, Cephalotaceae, Cistaceae, Corynocarpaceae, Cucurbitaceae, Elaeagnaceae, Juglandaceae, Lythraceae, Moringaceae, Myrothamnaceae, Pandaceae, Passifloraceae, Polygalaceae, Rhoipteleaceae, Rutaceae, Sabiaceae, Saururaceae, Saxifragaceae, Styracaceae, Turneraceae.
54	Aextoxicaceae, Ancistrocladaceae, Araliaceae, Basellaceae, Burseraceae, Datiscaceae, Linaceae, Myrsinaceae, Nyssaceae, Onagraceae, Opiliaceae, Punicaceae, Scytopetalaceae, Zygophyllaceae.
55	Proteaceae.
56	Eucommiaceae.
57	Aceraceae, Actinidiaceae, Caricaceae, Crassulaceae, Droseraceae, Empetraceae, Geraniaceae, Hippocastanaceae, Plumbaginaceae, Tovariaceae.
58	Alangiaceae, Bretschneideraceae, Capparidaceae, Daphniphyllaceae, Dichapetalaceae, Gomortegaceae, Malpighiaceae, Moraceae, Penaeaceae, Polygonaceae, Symplocaceae, Vochysiaceae.
59	Nyctaginaceae.
60	Casuarinaceae, Piperaceae.
61	Asclepiadaceae, Caryophyllaceae, Convolvulaceae, Halorrhagaceae, Thelygonaceae, Tropaeolaceae.
62	Amaranthaceae, Coriariaceae, Cyrillaceae, Heteropyxidaceae, Hydrocaryaceae, Oliniaceae, Salvadoraceae, Trigoniaceae.
63	Strasburgeriaceae.
64	Apocynaceae, Aquifoliaceae, Boraginaceae, Cruciferae, Diapensiaceae, Ericaceae, Pittosporaceae, Rubiaceae, Sarraceniaceae.
65	Bruniaceae, Frankeniaceae, Icacinaceae, Lissocarpaceae, Olacaceae, Stackhousiaceae.
67	Balanopsidaceae, Byblidaceae, Diclidantheraceae, Geissolomataceae, Hoplestigmataceae.
68	Caprifoliaceae, Epacridaceae, Limnanthaceae, Loasaceae, Oleaceae, Roridulaceae, Umbelliferae.
69	Achariaceae, Fouquieraceae, Theophrastaceae.
70	Podostemonaceae.
71	Clethraceae, Compositae, Cornaceae, Loganiaceae, Octoknemataceae, Rafflesiaceae.
73	Ceratophyllaceae, Crypteroniaceae, Malesherbiaceae, Pirolaceae.
75	Balsaminaceae, Batidaceae, Calyceraceae, Chloranthaceae, Desfontaineaceae, Loranthaceae, Myoporaceae, Nolanaceae, Primulaceae, Solanaceae, Stylidiaceae.
77	Chenopodiaceae, Santalaceae.
78	Julianaceae.
79	Garryaceae, Hydrophyllaceae, Polemoniaceae.
80	Hydnoraceae.
81	Lennoaceae.
82	Brunoniaceae, Campanulaceae, Dysphaniaceae, Gentianaceae, Goodeniaceae, Scrophulariaceae.

Advancement Index %	
83	Globulariaceae, Grubbiaceae, Myzodendraceae.
85	Cynomoriaceae.
86	Acanthaceae, Adoxaceae, Labiatae, Plantaginaceae.
88	Columelliaceae.
90	Callitrichaceae.
92	Balanophoraceae, Phrymaceae.
93	Bignoniaceae, Gesneriaceae, Lentibulariaceae, Orobanchaceae, Verbenaceae.
96	Dipsacaceae, Pedaliaceae.
100	Hippuridaceae, Hydrostachyaceae, Martyniaceae, Valerianaceae.

It is interesting to see that the Valerianaceae and the Dipsacaceae are highly placed in this list, for Stebbins also concludes that, among others, they represent "the highest degree of specialization of the angiosperm flower and fruit." It is even more interesting, perhaps, to discover which families are the most primitive and approach most nearly to the ancestral dicotyledon. Among the eight most primitive families, there are representatives of five distinct orders: Ranales, Malvales, Parietales, Rosales and Myrtiflorae. The Ranalian family Magnoliaceae is the most primitive of all, but it seems likely that the other four orders started to diverge from the ancestral type very early in angiosperm evolution.

These conclusions remain substantially the same, even if all the eighteen characters from Table I are used, for the lower end of the series would then read as follows:

Advancement Index %	
13	Myristicaceae.
19	Magnoliaceae, Euphorbiaceae.
23	Flacourtiaceae, Platanaceae.
25	Leguminosae, Malvaceae, Sapindaceae.
26	Bombacaceae.
28	Anonaceae, Rhamnaceae, Tiliaceae, Trochodendraceae.

From this, it would appear that the Myristicaceae are more primitive than the Magnoliaceae, but this is just one of the disadvantages of taking the family as the statistical unit, instead of the genus, for the figure quoted is merely an average for the family and within that family there may be some genera much more advanced and some much more primitive. Comparing genera by this method, it is found that several members of the Magnoliaceae (as defined by Engler and Diels) are more primitive than the Myristicaceae. Thus, *Magnolia* and *Schizandra* have an advancement index of 5.5 and *Drimys* one of 11.

It will come as no surprise to many botanists to read that the Magnoliaceae are nearer than any other living family to the ancestral type of dicotyledon. It is important to realise, however, that this conclusion no longer rests on preconceptions of hypothetical "proto-angiosperms," nor on any supposed derivation of floral organs from foliage leaves. It has been reached by logical processes which reduce to a minimum the personal factor. These same logical processes have also established the existence of trends in the subsequent evolution of dicotyledons. While it is not proposed to embark on a discussion of the mechanisms which might be responsible for these trends, it is presumed that Stebbins is correct in regarding them in terms of biological efficiency. Most of the trends are in accordance with commonly held beliefs, but there is one which proves unacceptable to many botanists, and this concerns the evolution of hermaphrodite from unisexual flowers. On examination, however, most of the arguments against this conclusion can be reduced to the mere expression of personal convictions. Looking at the matter dispassionately, it is difficult to discover any real objection to the suggestion that the ancestral dicotyledon was unisexual. Most botanists would agree that angiosperms had their origin among gymnosperms, yet there are only two gymnospermous groups with hermaphrodite members (Bennettitales and Gnetales) neither of which is a probable ancestor for the angiosperms.

It is true that both groups have, at one time or another, been claimed as such, but a close examination of the reproductive organs of the Bennettitales proves them to be most unpromising as a starting point for the evolution of any angiospermous flower, while the absence of vessels from some of the most primitive angiosperms (*Drimys* and *Trochodendron* inter alia) indicates that the Gnetales are equally unpromising.

Parkin (1952) has criticised the derivation of hermaphrodite from unisexual flowers on the grounds of the difficulty of visualising how the change could have occurred. "How," he says, "do those botanists who favour the primitive angiospermous flower as being unisexual derive the bisexual (hermaphrodite) one from it?" He then, jokingly, says, "Shall we imagine a saltation which resulted in the female flower taking a leap, as it were, and landing on the tip of the male, and shedding its perianth members in the process?" If there is a problem at all, it has also to be faced in gymnosperm evolution, yet it seems to have caused little concern to students of that group. A simple genetic change from diploid to tetraploid results in the production of hermaphrodite flowers in *Empetrum nigrum* agg. (Hagerup, 1927), so why should not similar changes have taken place elsewhere among seed plants? The change must presumably have been a sudden one like this, for it is inconceivable that it could have been gradual, whether it took place at the gymnosperm or at the angiosperm level of evolution, since any biological advantage which there may be in the hermaphrodite flower is only expressed if such flower is completely functional. Subsequent reversion to the unisexual condition, however, could well have been a gradual process, during which rudiments of the opposite sex could persist. Rudiments, then, are to be taken as characteristic of the first stages in the process leading to complete absence of rudiments. Unisexual flowers which lack rudiments of the opposite sex may, therefore, as already mentioned, represent one of two alternatives—either a primitive condition or an extremely advanced one. Now, a scrutiny of the families listed above as primitive, brings to light a fact which is of the greatest significance in this respect. Neither in *Schizandra* nor in *Myristica* do rudimentary sex organs occur. In view of the extreme primitiveness of these two genera, it is difficult to regard their unisexuality as anything other than a primitive survival of the ancestral condition.

Returning, now, to the consideration of Stebbins' views in relation to my own, it will at once be realized that we have focussed attention on opposite ends of the evolutionary scale. Stebbins was primarily interested in the most advanced families as being the highest expression of biological efficiency, whereas I was more interested in the most primitive families as being possible pointers to the ancestors of flowering plants. As to the most advanced families, we are in rough agreement. The hypothesis that parallel trends have occurred in evolution, assumed by Stebbins to be true, is actually proved to be so by statistical analysis, and, with some notable exceptions, we are in agreement as to the direction which these trends have taken. Finally, the fact, demonstrated by Stebbins, that certain character combinations are rarer than others, on structural or functional grounds, has provided a welcome explanation of certain inconsistencies in the results of statistical analysis which were otherwise rather puzzling. Thus, far from being irreconcilable, our views are, in fact, complementary. The truth of Stebbins' remark that "the problem of the primitive flower cannot be settled by statistics alone" cannot be denied, but nevertheless, in our present state of knowledge, it does offer one of the most hopeful means of approach to the problem.

Summary

Statistical correlation between floral and vegetative characters possessed by the families of dicotyledons may arise from

a number of contributing factors, of which the most important are: (1) the characters are concerned in evolutionary trends and are indicators of primitiveness or advancement, (2) the characters are associated in a direct functional way with each other. In the absence of the second factor, all primitive characters (and also all advanced) would be expected to show positive correlation when taken in pairs. The fact that this is not universally the case suggests that the second factor operates to a greater or lesser extent, according to the number of discrepancies thereby produced. The characters which show the fewest discrepancies and are, therefore, the most reliable indicators of primitiveness are: woody habit, presence of secretory cells, leaves alternate, stipules present, flowers actinomorphic, petals free, stamens pleiomerous, carpels pleiomerous, seeds arillate, two integuments, integumentary vascular bundles, nuclear endosperm, carpels free, axile placentation. On the basis of these fourteen characters, the most primitive families of dicotyledons are: Magnoliaceae, Bombacaceae, Flacourtiaceae, Anonaceae, Leguminosae, Malvaceae, Myristicaceae. The most advanced are: Dipsacaceae, Pedaliaceae, Hippuridaceae, Hydrostachyaceae, Martyniaceae, Valerianaceae. Three further characters are believed to have been present in ancestral dicotylendons and, therefore, are primitive in certain families, but have also appeared secondarily in certain advanced families. These are: unisexual flower, haplochlamydy and small number of seeds. Axile placentation is primitive among families with several fused carpels, but is a character difficult to assess correctly in highly modified ovaries. When these four characters are used in conjunction with the previous fourteen, the most primitive families are found to be Myristicaceae, Magnoliaceae, Euphorbiaceae, and Flacourtiaceae. The most primitive genera are *Magnolia*, *Schizandra* and *Drimys*.

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ISOLATION IN MUSA, SECTIONS EUMUSA AND RHODOCHLAMYS

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Introduction

Musa is an Asian genus which has recently been classified by Cheesman (1947) in four sections: Australimusa and Callimusa with n = 10, Eumusa and Rhodochlamys with n = 11 chromosomes. All the known wild species are diploid and collections of many of them have been built up over the past thirty years at the Imperial College of Tropical Agriculture, Trinidad, for taxonomic and cytogenetic study and for breeding purposes. Many interspecific hybridizations have been made, with the result that we now have a fairly complete picture of cytogenetic relations within and between the 11-chromosome sections, Eumusa and Rhodochlamys. This paper summarizes the results from the viewpoint of interspecific isolation and is concerned solely with the wild, seeded bananas. Edible forms will not concern us here except as objects of passing reference at the end of the discussion.

The author is deeply indebted to his predecessors in banana research at this Institution, Drs. E. E. Cheesman and K. S. Dodds, not only for their help and guidance in the past but also for the numerous data of theirs which are incorporated in this report.

Plant Materials

Eight species were used, as follows:

Section Eumusa

1. *Musa acuminata* Colla. An extremely variable species with a wide geographical distribution from Burma through Malaysia to New Guinea, Queensland, Samoa and the Philippines. Several races have been distinguished by Cheesman (1948; and see Simmonds, 1952) of which two have been used in this study. The Selangor (Malayan) form (represented by Clone A, Introduction 53) has been taken as standard and its use is implied unless a contrary statement is made. The Tavoy (Burmese) form (represented by the clone Calcutta 4, Introduction 124) differs from the Selangor in many genes and two interchanges (Dodds & Simmonds, 1948a; Simmonds, 1952, 1953); passing reference will be made to it here. Cheesman also distinguished the Mariani form from Assam, noting that it might ultimately have to be segregated as a distinct species. Later studies (Simmonds, 1952 and unpublished) support such a segregation and the form has therefore been excluded from consideration, an exclusion which, of course, restricts the geographical distribution of *M. acuminata* in the limited sense.

2. *Musa balbisiana* Colla. The most widely ranging banana species, distributed from Ceylon, through India, Assam, Burma and Malaysia to New Guinea and the Philippines. The species is but slightly variable and has been represented almost exclusively by one clone (Clone Ceylon, Introduction 100, from Ceylon) in this work.

3. *Musa basjoo* Sieb. Native to the Liukiu archipelago of southern Japan, this is the most northerly and hardy species of *Musa*, very distinct in phenotype and distribution from all other bananas. One clone has been used (Introduction 78A, from Devonshire, England, a cultivated plant).

4. *Musa itinerans* Cheesm. Known only as one clone (Introduction 184) from Upper Burma, the living type specimen upon which Cheesman described the species.

Section Rhodochlamys

5. *Musa laterita* Cheesm. Known only from southwestern Burma. One clone (Introduction 225) has been used in this work and is the living type specimen upon which Cheesman described the species.

6. *Musa ornata* Roxb. The natural distribution of this species is uncertain but most probably it occurs in the East Pakistan-southern Assam-west central Burma region. One clone (Introduction 1, of botanic gardens origin) has been used.

7. *Musa sanguinea* Hook. f. Native of Assam. One clone has been used (Introduction 207).

8. *Musa velutina* Wendl. & Drude. Native of Assam. One strain (jointly vegetatively- and seed-propagated) has been used (Introduction 212).

Results

Geographical and ecological isolation

Information on geographical isolation of components of the twenty eight pairs of species is given in Table 1. Unfortunately, knowledge of the geographical distribution of the species is so fragmentary that it is often not possible to make more than an informed guess as to whether any two species live in the same area or not; the data of table 1 therefore represent the best current estimate of the situation but are liable to be modified by future investigations.

Knowledge of the ecology of the wild bananas is also fragmentary, but probably they are all plants of streamsides and clearings in forests at low or, at most, middle altitudes. Unless growth is severely checked by drought or other cause, they flower all the year round. The basal flower clusters of each inflorescence are female (exceptionally hermaphrodite as in *M. velutina* and some forms of *M. acuminata*); the upper flower clusters are male, the pollen is sticky and pollination is presumably mainly by insects.[1]

Table 1 shows that eight pairs of species are sympatric (i.e. inhabit the same geographical area), thirteen are probably or possibly sympatric, and seven are certainly or nearly certainly allopatric. These seven, however, all involve *M. basjoo* and if it be excluded from consideration, it becomes probable that the degree of sympatry among the remaining seven species is high. This conclusion, however, could be seriously wrong if geographical distri-

[1] Humming birds are conspicuous flower visitors in Trinidad.

TABLE 1. *Isolation between species of* Musa *I. Geographical and early stages of reproductive isolation.* Upper right—geographical isolation: 1—certainly or nearly certainly sympatric; 2—possibly or probably sympatric; 3—allopatric. Lower left—reproductive isolation up to the mature hybrid zygote: 1—cross easy (at least one way) and hybrids viable, natural hybridity possible; 2—cross difficult and/or hybrids weakly, natural hybridity doubtful; 3—cross so difficult and/or hybrids so weakly that natural hybridity impossible or at least very unlikely.

	Eumusa				Rhodochlamys			
Species	ac	bb	bj	it	lat	orn	san	vel
Eumusa								
*acuminata**	—	1(1)	3(3)	3(2)	3(1)	3(2)	3(2)	3(2)
balbisiana	1	—	3	1	1	1	1	1
basjoo	3	2	—	3	3	3	3	3
itinerans	1	3	1	—	2	2	2	2
Rhodochlamys								
laterita	1	1	3	3	—	2	2	2
ornata	1	3	3	3	2	—	2	2
sanguinea	3	2	3	3	3	3	—	1
velutina	2	2	3	3	1	1	1	—

* The first entry in each cell in this line refers to the Selangor form of the species, the entry in brackets to the Tavoy form.

butions were much more restricted than the present enlightened guesswork indicates. It is likely that the sympatric pairs grow in similar ecological situations, flower at the same time and are therefore, sometimes at least, liable to cross pollination by insects. Interspecific pollination in nature must be a relatively common event. Cheesman (1948) has recorded the existence of a natural hybrid between *M. balbisiana* and *M. nagensium* and natural crossing between wild species in cultivation is quite a common occurrence.

Crossability and hybrid viability

In table 1 data are presented in the form of figures estimating in a fairly crude fashion the likelihood of viable F_1 plants being established if the requisite interspecific pollination has taken place. They are based on records of more than twenty years of experimental pollination, of the seeds set, of germinations obtained, and of the growth and vigour of the hybrids. All crosses have been attempted in both directions and in some instances many hundred ovaries have been pollinated. Condensed results are summarized in the appendix.

Experiments in which interspecific pollinations were made and the numbers of swollen ovules counted after 7–10 days show that pollen tube growth and fertilization were essentially normal in every combination tested. Since all the fifty-six possible combinations of eight species have not yet been tested and since a year or so must elapse before the results are complete, details of these experiments will be reported elsewhere. At present it seems that failure of seed set is a consequence of failure of post-fertilization events rather than of haplo-diploid interaction in the style or of haplo-haploid interaction in the embryo-sac.

All 28 hybridizations have yielded seed in one direction or the other (in most cases in both directions), though there were considerable differences in the ease of crossing as between pairs of species. Hybrid viability varied considerably from a high level down to cases in which the seed did not germinate or the young F_1 seedlings died. There were several instances in which the strain of *M. acuminata* used affected the results, hybrids of the Tavoy (Burmese) form with Rhodochlamys species being less vigorous than the corresponding Selangor (Malayan) crosses (Appendix, entries 4 and 5). Reciprocal differences in crossability or hybrid viability probably sometimes occur and several are noted in the appendix; the combination *M. basjoo*-Rhodochlamys is a conspicuous instance, the crosses being very much easier when *M. basjoo* is the female parent. In another, less extreme, instance, that of *M. ornata* × *M. velutina*, experiments showed that *M. ornata* pollen on *M. velutina* gave 6.6% of the seed yield obtained by selfing whereas *M. velutina* pollen on *M. ornata* gave 26.3%; the cause is unknown but the fact is clear that the cross is four times as successful one way as the other.

The general conclusion seems to be that all hybridizations can be made but that F_1 viability varies greatly; that some species are more isolated from other members of their own section than they are from the more nearly related members of the other section; and that there are minor complications due to differences between strains within a species and to certain reciprocal differences.

Hybrid cytology

Observations of male cytology of the hybrids were made on aceto-carmine smear preparations and, where possible, 20 first metaphases and 50 anaphases were analysed; data from reciprocal and related crosses have been combined in several entries but it should be noted (see below) that only one hybrid of the Tavoy (Burmese) race of *M. acuminata* has contributed to the data summarized in table 2 (see footnote (5)).

Meiosis varied from normal or nearly so (e.g. *M. basjoo* × *M. itinerans*, *M. ornata* × *M. velutina*, each with nearly normal pairing but heterozygous for inversion) to very irregular (e.g., *M. laterita* ×

TABLE 2. *Isolation between species of* Musa II. *The later stages of reproductive isolation*

Hybrid	Cytology (1)	Fertility (2)	Progeny (3) 2x	3x	5x
Within Eumusa					
M. acuminata × *M. balbisiana*	1.44 (I)	0.51	0	0	20
M. acuminata × *M. basjoo*(5)	6.4	0.76	1	0	0
M. acuminata × *M. itinerans*	3.80 (I)	14.1	—	—	—
M. balbisiana × *M. basjoo*	3.32(TI)	1.67	15	0	0
M. basjoo × *M. itinerans*	0.00 (I)	8.34(4)	—	—	—
Within Rhodochlamys					
M. laterita × *M. ornata*	10.70 (I)	0.80	3	0	1
M. laterita × *M. velutina*	2.67 (I)	0.22	—	—	—
M. ornata × *M. velutina*	0.50 (2I)	179.5	102	0	2
M. sanguinea × *M. velutina*	1.30	34.2	21	0	0
Between Eumusa and Rhodochlamys					
M. acuminata × *M. laterita*	1.50(2T)	38.2	87	0	0
M. acuminata × *M. ornata*	2.57(1–2I)	49.7	8	4	135
M. acuminata × *M. sanguinea*	—	7.35	—	—	—
M. acuminata × *M. velutina*	2.17(2I)	57.8(4)	0	0	102
M. balbisiana × *M. laterita*	8.60(T)	24.0	2	81	111
M. balbisiana × *M. ornata*	3.59(I)	0.19	—	—	—
M. balbisiana × *M. sanguinea*	12.80	0.00(4)	—	—	—
M. balbisiana × *M. velutina*	9.05(T)	0.00(4)	—	—	—

Notes: (1) Univalents per first metaphase nucleus; in brackets the occurrence of multivalent associations (T) and anaphase bridges with fragments (I). (2) Fertility of hybrids on haploid pollination (usually backcross), as seeds per 1000 ovules. (3) Numbers of plants in each category of ploidy indicated. Determinations mostly by chromosome count, sometimes by examination of stomata. All available data, published and unpublished, are incorporated, including some from hybrids of the Tavoy form of *M. acuminata*. A few aneuploids (e.g. 2n = 32,34) have not been specially distinguished. (4) Fertilities based on fewer than 10,000 ovules and therefore rather unreliably known. (5) Data mainly from Dodds and Pittendrigh (1945). The clone has since died; it was a hybrid of *M. basjoo* with the Tavoy form of *M. acuminata*.

M. ornata and *M. balbisiana* × *M. sanguinea*, each with a high degree of failure of pairing).

Multiple associations were seen in several hybrids and are assumed to result from translocation; as is usual in *Musa*, the interchanges rarely formed complete associations so that estimates of their numbers are necessarily minimal (Dodds & Simmonds, 1948a). Bridges and fragments were common and were assumed to be caused by inversion. Bridges without fragments were also seen sometimes but their presence has not been recorded in table 2; they may have resulted from stickiness of the chromosomes or from various minor structural changes (e.g. inversions so small as to give an invisible fragment). Data from the hybrid *M. ornata* × *M. velutina* (S.H. 69) illustrated their occurrence and show also the consequences of complementary double chiasmata in a large inversion:

First Anaphases with:

No bridge	Bridge and fragment	Bridge and 2 fragments	Bridge alone
52	19	2	6

Evidently, cytological differentiation, both gross and cryptic, has occurred in the course of speciation. Cytological differences between Eumusa and Rhodochlamys are perhaps greater, but not very much greater, than between species within one section, essentially the same conclusion as was drawn above with regard to crossability.

TABLE 3. *Hybrids of two forms of* M. acuminata *with various wild species.* Mean numbers of univalents per nucleus at first metaphase with (brackets) minimal numbers of interchanges.

	M. balbisiana	*M. itinerans*	*M. ornata*	*M. laterita*
Selangor	1.44 (1)	3.80 (0)	2.57 (0)	1.50 (2)
Tavoy	5.00 (2)	5.15 (1)	3.46 (2)	0.85 (1)

In four instances, hybrids of both the Selangor and Tavoy forms of *M. acuminata* with other wild species were available for comparison and in three of them the hybrid with the Tavoy form had the higher frequency of univalents and multivalents (table 3). This can be related to the fact (Dodds & Simmonds, 1948a) that the Selangor-Tavoy hybrid is heterozygous for two interchanges although the parents are homozygous. Evidently, interchange has accompanied racial differentiation within *M. acuminata* and the chromosomes of the other wild species are homologous with those of the Selangor rather than with those of the Tavoy form. This conclusion may be compared with the observation (above) that Rhodochlamys-Tavoy hybrids are less viable than Selangor-Tavoy hybrids. Jointly they indicate that the Tavoy chromosome pattern had no part in the general differentiation of the 22-chromosome bananas.[2] Either it existed but was isolated from these events or it is of later origin; the latter perhaps is more likely in view of the comparatively slight difference between the Tavoy and the Selangor forms.

Hybrid fertility

Most of the hybrids raised to maturity have been tested for fertility by pollination by one or both of the parent species. Results are given in table 2 as seeds per 1000 ovules. For comparison it may be noted that the wild species yield about 4–800 seeds per 1000 ovules so that only one of the hybrids approached 50% female fertility (*M. ornata* × *M. velutina*); the rest were much less fertile but rarely completely sterile and experience suggests that all would ultimately yield a few seeds if enough pollinations were made. Once again the species seem to be nearly as highly differentiated within sections as between them and, indeed, several intersectional crosses appear to be distinctly more fertile than hybrids within Eumusa at least.

Backcross and F_2 generations

Most of the tests of F_1 fertilities were made as backcrosses with haploid pollen from one or both parents; many seeds were sown and results of determinations of the ploidy of the progeny are summarized in the last three columns of table 2. Diploids, triploids and pentaploids were found in varying proportions, the polyploids among them having originated by a process of restitution peculiar to and characteristic of *Musa* hybrids (Dodds & Pittendrigh, 1945; Dodds & Simmonds, 1946). The cytological details need not concern us here. It will suffice to state simply that the process is rarely seen on the male side, so that male cytology may be a poor guide to female behaviour; that polyploid spores are functional only on the female side; that there are differences between siblings of one cross and even between bunches of one clone in the relative frequencies of the various classes (Dodds & Simmonds, 1946; Simmonds, 1948). Now, the polyploids are presumably an evolutionary dead-end for the triploids are highly infertile and the pentaploids very weak. The diploid seedlings alone could have evolutionary significance, so that the *effective* fertility of a hybrid is the number of viable diploid zygotes it produces, not the number of seeds or even viable seeds. On this basis, only four hybrids, two within Rhodochlamys and two intersectional crosses, are appreciably fertile and there are two conspicuous instances where an apparently high fertility is, in the evolutionary sense, spurious in that the backcross seedlings are predominantly poly-

[2] With the possible exception of *M. laterita*—table 3.

ploid (*M. acuminata* × *M. velutina* and *M. balbisiana* × *M. laterita*). In these cases, polyploid female spore production is probably the *cause* of high female fertility, in that it provides an escape from the normal consequences of meiotic misbehaviour; indeed, whenever high female fertility is associated with much failure of male meiotic pairing there is good *a priori* reason to suspect that the backcross progeny will be polyploid.

To what extent the frequency of diploid progeny is characteristic of a whole cross rather than merely of a clone is not known. Certainly, different clones of various parentage within the cross *M. acuminata* × *M. ornata* showed markedly different frequencies of diploids in their progeny, just as siblings within one family also showed variation in this respect (see above). Probably, female restitution reduces somewhat the effective (i.e. diploid) zygote production of many if not all these hybrids but does not impose complete sterility with respect to diploid progeny on any whole interspecific parentage.

Polyploid spore production is in effect, then, an isolating mechanism comparable in evolutionary effect with the genetic breakdown of the F_2 known to occur in certain other plants. In bananas, diploid backcross families have not been raised to maturity and the only known interspecific F_2 is that between *M. ornata* and *M. velutina* of which a family has been described by Simmonds (1953). The great majority were diploid, most were vigorous and some were highly fertile. Genetical variation was evidently polygenic in character. Thus there was no pronounced genetic breakdown in the F_2 and there is little doubt that some of the most vigorous and fertile segregates could have survived and reproduced in nature; the parents are not effectively reproductively isolated and we therefore have no evidence of the operation of this mode of isolation in *Musa*, though it is being sought and may well be found in other crosses.

Discussion

The centre of diversity

Seven out of the eight banana species studied are native in (but not necessarily confined to) the Assam-Burma region; the eighth, *Musa basjoo*, is native to southern Japan. One other 22-chromosome species (*M. nagensium* Prain) is known and a few others are suspected to exist (Cheesman, 1947); all (with the possible exception of an unidentified form in peninsular India) come from the north-eastern India-Assam-Burma-Siam region. This, then, is the centre of diversity of the group and it may be worth noting that the 20-chromosome sections, though ranging into Malaya, Indo-China and Siam, are distinctly more southern and eastern in distribution.

Relationships

We have seen that reproductive isolation between species within a section is comparable in magnitude with that between species belonging to different sections; in other words, each section is nearly as much differentiated within itself as it is differentiated from the other section, if we use degree of reproductive isolation as a measure. Taxonomy (which here represents a singularly clear and natural sectional grouping) is not, therefore, a certain guide to genetic relationship, for example: *Musa acuminata* (Eumusa) is clearly much more nearly allied to *M. laterita* (Rhodochlamys) than it is to *M. basjoo* (Eumusa) and similarly, *M. laterita* to *M. acuminata* than to *M. ornata* (Rhodochlamys). Striking amplification of this result comes from experiments (Simmonds, 1952, and unpublished) which show the so-called Mariani form of *M. acuminata* (Cheesman, 1948) to be closely allied to certain Rhodochlamys species but sharply differentiated from *M. acuminata* which it undoubtedly resembles phenotypically.

The genetic relationships of the eight species studied here are summarized in the diagram, Fig. 1, in which linear dis-

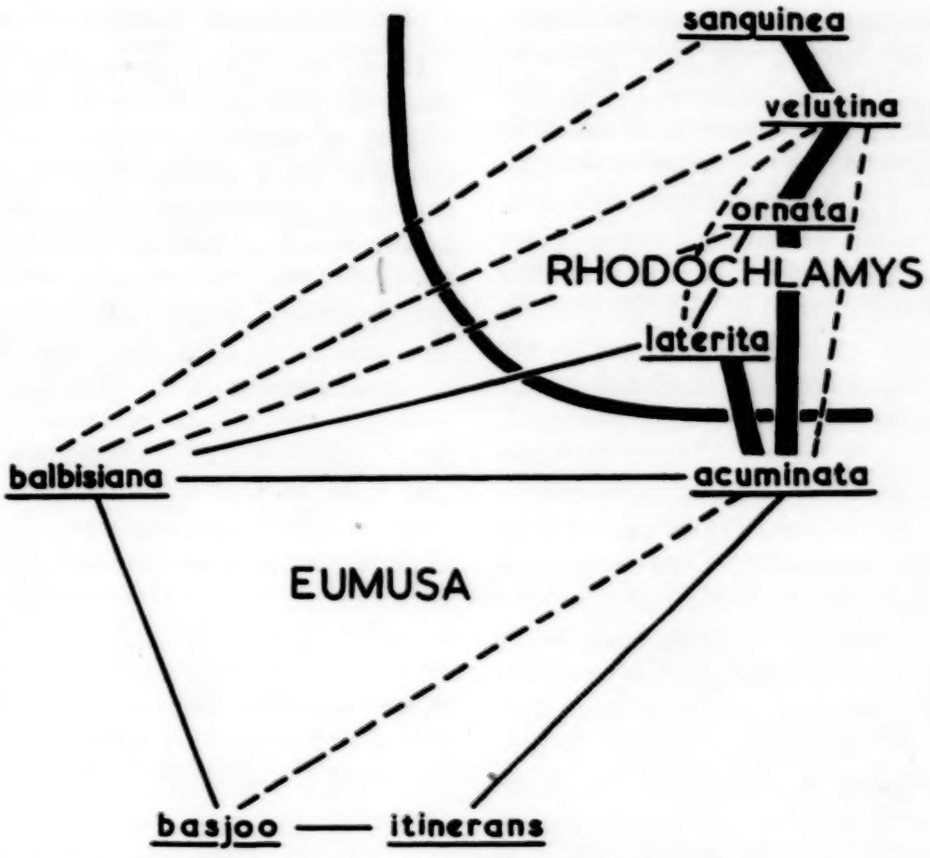

FIG. 1. Relationships among the wild 22-chromosome bananas, sections Eumusa and Rhodochlamys.

tances roughly represent the level of differentiation indicated by the data on reproductive isolation given in tables 1 and 2.

In Eumusa, *M. basjoo* and *M. itinerans* constitute a distinct pair of related species which resemble each other in their widespreading rhizomes and distance of relationship to Rhodochlamys. *M. balbisiana* is effectively isolated from all the others and has no apparent close affinities. *M. acuminata* of these four Eumusas, approaches Rhodochlamys most nearly and indeed is nearer to *M. laterita* than it is to any Eumusa studied; however, it should be noted that the Tavoy (Burmese) form of the species is more isolated from Rhodochlamys than is the Selangor form (see sections 3 (b) and (c) and below). In Rhodochlamys, *M. laterita* approaches the Eumusoid *M. acuminata* but is rather distinct from the other three species. The section appears to be less highly differentiated than Eumusa. All members of Rhodochlamys have small geographical ranges and this contrasts with the greater intrasectional differentiation of Eumusa and the wider ranges of some of its species; hence Rhodochlamys seems to be the evolutionarily younger group and its origin from some *acuminata*-like ancestor is indicated.

Isolation

These eight species exhibit a rather wide range of modes of isolation, including: geographical isolation, inviability of hybrid zygotes at various stages from inception to maturity, and F_1 sterility and meiotic breakdown. We have at present no evidence of ecological isolation, of barriers to pollination or fertilization, or of an F_2 genetic breakdown but these are being sought and may yet be found.

Of all the 28 pairs of species, only four appear to be possible or probable instances

of non-isolation, thus: (1) *Musa acuminata* and *M. laterita* are very probably sympatric in Lower Burma. The Selangor form of *M. acuminata* shows little or no reproductive isolation from *M. laterita* but is probably not sympatric with it; the Tavoy (Burmese) form gives much less vigorous hybrids and since this is the form with which *M. laterita* is probably in contact in the field, the species are likely to be effectively isolated. (2) *Musa acuminata* and *M. ornata* are possibly sympatric in Burma. Much the same considerations apply here as in the previous case—reproductive isolation between the possibly sympatric forms is greater than between the allopatric ones, so that the two species are probably isolated in nature. (3) *Musa ornata* and *M. velutina* are possibly or even probably sympatric in Assam or northeastern India. Reproductive isolation is slight and the F_2 is vigorous (Simmonds, 1953). Introgression seems likely if the parents are sympatric. (4) *Musa sanguinea* and *M. velutina* are probably sympatric in Assam and reproductive isolation is slight. Again, introgression seems likely. Thus the only two really likely instances of non-isolated pairs occur within Rhodochlamys and this is clearly to be related to the lesser degree of differentiation of this section as compared with Eumusa.

It may be concluded that the existing variety of modes of isolation are generally effective in maintaining specific integrities. This is not to say that the same variety of modes were operative in the speciation process. Indeed it seems likely, on *a priori* grounds, that geographical isolation was of primary importance and that reproductive isolation followed secondarily, accumulated step by step as an inevitable consequence of differentiation. In this connection it is perhaps significant that the centre of diversity is predominantly mountainous and therefore, presumably, favourable to geographic isolation.

The importance of Musa acuminata

Of all these wild species, we have evidence of only two being involved in the origins of edible bananas. Edibility is procured by a combination of genes for vegetative parthenocarpy (i.e. autonomous production of a starchy locular pulp without pollination) and female sterility, additional sterility being imposed sometimes by structural hybridity and triploidy. *Musa acuminata* is the principal (indeed probably the only) source of parthenocarpy among the 22-chromosome bananas and it is from this species, alone and in various hybrid combinations with *M. balbisiana*, that at least the bulk of the edible banana complex has evolved under human selection (Dodds & Simmonds, 1948a, b; Simmonds, 1953). Thus *M. acuminata* is incomparably the most complex, interesting and important species by reason of its being the primary source of a major crop.

Summary

The sections Eumusa and Rhodochlamys are composed of diploid species with 22 chromosomes and have a centre of diversity in the Assam-Burma region. Geographical distributions, crossing relationships, fertility and breeding behaviours of F_1 hybrids are described for the 28 possible combinations of eight species, four from each section. Geographical and various modes of reproductive isolation occur. Isolation appears to be complete except between two pairs of species of Rhodochlamys. Eumusa is more highly differentiated than Rhodochlamys and is thought to be the older group.

Appendix

Summary of data on geography and crossability

1. ACUMINATA × BALBISIANA. *Geography*—sympatric from Burma to New Guinea; *crossing* easy, both ways; *germination* variable; *hybrids* fairly vigorous (B × A) or rather weakly (A × B), a possible reciprocal difference.
2. ACUMINATA × BASJOO. *Geography*—allopatric; *crossing* rather easy, both ways; *germination* poor or bad; *hybrids* (A ×

Bjoo and Bjoo × A) often inviable as seedlings; mature plants inviable or weakly, rarely flowering.

3. ACUMINATA × ITINERANS. *Geography*—possibly sympatric in upper Burma; *crossing* quite easy, both ways; *germination* fair; *hybrids* fairly vigorous (A × I and I × A).
4. ACUMINATA × LATERITA. *Geography*—very probably sympatric in lower Burma; *crossing* very easy, both ways; *germination* good; *hybrids* (A × L and L × A) vigorous (but hybrids of the Burmese race of *M. acuminata* represented by clone Calcutta 4 (I.R. 124) with *M. laterita* are much less vigorous).
5. ACUMINATA × ORNATA. *Geography*—possibly sympatric in middle Burma or neighbouring East Pakistan; *crossing* easy, both ways; *germination* good; *hybrids* (A × O and O × A) vigorous (but hybrids of the Burmese race of *M. acuminata* represented by clone Calcutta 4 (I.R. 124) with *M. ornata* (A × O) were narrow-leaved weakly seedlings).
6. ACUMINATA × SANGUINEA. *Geography*—possibly sympatric in Assam; *crossing* easy, both ways; *germination* bad; *hybrids* (S × A and A × S) hardly viable, rarely reaching maturity and then difficult to keep alive.
7. ACUMINATA × VELUTINA. *Geography*—possibly sympatric in Assam; *crossing* easy, both ways; *germination* fair; *hybrids* weakly as seedlings (A × V and V × A), survivors (A × V) fairly vigorous at maturity.
8. BALBISIANA × BASJOO. *Geography*—allopatric; *crossing* easy, but many empty seeds occur; *germination* poor; *hybrids* show a probable reciprocal difference—Bjoo × B inviable as seedlings or survive and grow slowly with poor colour; B × Bjoo rather more vigorous and with better colour.
9. BALBISIANA × ITINERANS. *Geography*—sympatric in upper Burma; *crossing* rather difficult both ways, perhaps easier as I × B; *germination* poor; *hybrids* (B × I and I × B) inviable as young seedlings.
10. BALBISIANA × LATERITA. *Geography*—sympatric in lower Burma; *crossing* quite easy, both ways; *germination* fair; *hybrids* (B × L) vigorous as mature plants, the reciprocal (L × B) much less vigorous, perhaps inviable.
11. BALBISIANA × ORNATA. *Geography*—sympatric in middle Burma or neighboring East Pakistan; *crossing* easy, both ways; *germination* fair; *hybrids* (B × O and O × B) weak or even inviable as seedlings and at maturity.
12. BALBISIANA × SANGUINEA. *Geography*—sympatric in Assam; *crossing* easy (B × S) or difficult (S × B); *germination* (B × S) good; *hybrids* usually inviable when young but survivors (B × S) fairly vigorous.
13. BALBISIANA × VELUTINA. *Geography*—sympatric in Assam; *crossing* easy, both ways (a series of failures is attributed to the very severe dry season of 1947); *germination* good; *hybrids* perhaps show a reciprocal difference, V × B rather more vigorous than the weakly B × V.
14. BASJOO × ITINERANS. *Geography*—allopatric; *crossing* easy, both ways; *germination* (B × I and I × B) good; *hybrids* (B × I) fairly vigorous, or (I × B) weakly or inviable, a probable reciprocal difference.
15. BASJOO × LATERITA. *Geography*—allopatric; *crossing* easy (B × L) or difficult (L × B); *germination* (L × B and B × L) bad; *hybrids* (B × L) very weakly at all stages, virtually "permanent seedlings" (though flowering rarely) after 5 years in the field; L × B unknown (no germinations).
16. BASJOO × ORNATA. *Geography*—allopatric; *crossing* easy (Bjoo × O) or very difficult (? impossible) (O × Bjoo); *germination* (Bjoo × O); very bad; *hybrids* inviable, the seedlings chlorotic.
17. BASJOO × SANGUINEA. *Geography*—allopatric; *crossing* easy (B × S) or very difficult (? impossible) (S × B); *germination* (B × S) very bad; *hybrid* (one B × S) inviable as a seedling.
18. BASJOO × VELUTINA. *Geography*—allopatric; *crossing* difficult; *germination* and hybrids unknown.
19. ITINERANS × LATERITA. *Geography*—possibly sympatric in middle Burma; *crossing* (L × I and I × L) easy; *germination* fair; *hybrids* (L × I and I × L) very weakly I × L perhaps worse than L × I.
20. ITINERANS × ORNATA. *Geography*—possibly sympatric in middle Burma; *crossing* easy (I × O) or rather difficult (O × I); *germination* poor; *hybrids* (I × O and O × I) inviable or nearly so, though (I × O) sometimes persisting for several years as non-flowering "permanent seedlings."
21. ITINERANS × SANGUINEA. *Geography*—possibly sympatric in upper Burma or Assam; *crossing* (S × I) difficult or (I × S) easy; *germination* poor; *hybrids* (I × S) and S × I) inviable as seedlings.
22. ITINERANS × VELUTINA. *Geography*—possibly sympatric in upper Burma or Assam; *crossing* (V × I and I × V) easy; *germination* bad to fair; *hybrids* (I × V) very weakly or inviable as seedlings.
23. LATERITA × ORNATA. *Geography*—possibly sympatric in middle Burma; *crossing* easy, both ways; *germination* variable, O × L fair, L × O very bad; *hybrids* (O × L) sometimes weakly and with

wrinkled leaves when young, quite vigorous at maturity, or (L × O, one plant) inviable as a young seedling.

24. LATERITA × SANGUINEA. *Geography* — probably allopatric; *crossing* rather easy (L × S) or difficult (S × L); *germination* bad; *hybrids* (two, S × L) inviable as seedlings, the reciprocal (L × S) unknown.

25. LATERITA × VELUTINA. *Geography*—probably allopatric; *crossing* easy, both ways; *germination* fair; *hybrids* probably show a reciprocal difference, L × V more vigorous than V × L.

26. ORNATA × SANGUINEA. *Geography*—possibly sympatric in Assam; *crossing* fairly easy, both ways; *germination* poor; *hybrids* (O × S and S × O) inviable as seedlings.

27. ORNATA × VELUTINA. *Geography* — possibly sympatric in Assam; *crossing* easy (O × V), perhaps less easy in reciprocal (V × O); *germination* good (O × V) perhaps less good in reciprocal (V × O); *hybrids* vigorous at maturity (O × V) or weak or inviable (V × O)—probably a true reciprocal difference. Segregation in an F_2 family has been described by Simmonds (1953).

28. SANGUINEA × VELUTINA. *Geography* — sympatric in Assam; *crossing* easy, both ways; *germination* good; *hybrids* vigorous (V × S) or weakly (S × V), a probable reciprocal difference.

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POPULATION DYNAMICS AND EVOLUTION

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INTRODUCTION

The student who embarks on the dynamics of populations follows an ancient trail; for we know that expectations of life were computed in classical Rome; and in the history of biometry, the life table was one of the earliest assets to be developed. The interest, however, was for long confined to human populations; then followed the laboratory studies of animal populations; and finally, quite recently, the students moved out into nature, and ecological study of the dynamics of natural populations was initiated.

In this final phase, which is as yet in its beginning, the ornithologists have blazed the trail, and to them is due most of the knowledge that we have of the dynamics of natural populations. There is, however, no real reason why this should be so. Many nonavian populations are excellently suited to this kind of study. But unfortunately the spread of ideas is painfully slow, owing to the deficient contact between specialized workers in different fields; and, though a few mammalogists and others are now contributing with fine studies, many possibilities are still left unheeded.

This is particularly the case with paleoecology. Yet mass occurrences of fossils, offering excellent material for this kind of research, are by no means uncommon. Neo- and paleoecologists, being in radically different positions, will necessarily have few methods of approach in common; the present one, however, they can share, with equal prospects of success on both sides.

An additional incentive to the paleontologists would perhaps be the prospect of having his say, with authority and assurance, on the *mechanics* of evolution, not only on its *history*—course and rate—as contemporary authoritative opinion is inclined to confine him to. No theory of selection is complete unless it states ***when*** and *how*, in the life history of a cohort, the selective factors operate; and the answers to these questions will in a large measure rely on the ecological disciplines of population dynamics and population control, respectively.

Population dynamics purport to study the distribution of mortality within a population, and to describe the survivorship, rate of mortality, and expectation of life, for its members. The results are generally condensed into a life table, which ideally follows the fate of a cohort from simultaneous fertilization to the death of the last survivor, giving, at regular intervals, the number of survivors, the number of deaths, the rate of mortality, and the mean remaining life time. Expositions of the life table treatment may be found, e.g. in Pearl (1940). Some important concepts are formulated by Pearl and Miner (1935). The classic on natural populations is Deevey's (1947) review. Among comprehensive recent ornithological contributions may be mentioned von Haartman (1951), Farner (1952), Hickey (1952).

In the present paper I intend to discuss some evolutionary implications of population dynamics, with special reference to fossil mammals. For a full account of the material and methods, the reader is referred to Kurtén (1953), on which most of the conclusions given here are based. The study concerns mainly samples of Lower Pliocene (*Hipparion* fauna) Chinese mammals in the Lagrelius collection, Uppsala. These fossils were deposited seasonally, and the samples could be split

into age groups one year apart in development, from biometric analysis of the state of wear of the dentition.

Age and Survivorship

It was one of the most remarkable discoveries of avian population dynamics that the rate of mortality in adults seemed to be independent of the age of the individuals. Thus, in the blackbird (*Turdus merula*) each adult age group will lose some 40 per cent of its members annually, regardless of whether it is made up by young adults or old. This generalization seems to be valid to a great extent for bird populations; it is called the "diagonal" survivorship pattern, as the corresponding survivorship curve, in the usual arithlog plotting, approaches a straight line. It is certainly not valid for all populations. The human survivorship curve is decidedly convex, with rates of mortality ascending steeply towards its termination; and the antithetic type, with high initial rates of mortality, which are reduced later in life, making the curve concave in outline, is probably exemplified in its extreme form by species with great output of young.

During the initial parts of life, rates of mortality seem in general to exceed adult rates. The magnitude of the difference is certainly variable. In the prawn, *Leander squilla,* the mortality from conception up to first reproductive period has been estimated on the order of 99.8 per cent (Kurtén, *op. cit.*). As the other extreme we may take civilized man, with a mortality of about 18 per cent from birth up to puberty. Tentative estimates for a number of natural mammal populations yield an average of some 70 per cent. In all these cases mortality is certainly reduced subsequently.

Adult mortality rates may persist fairly constantly through a great part of life; as

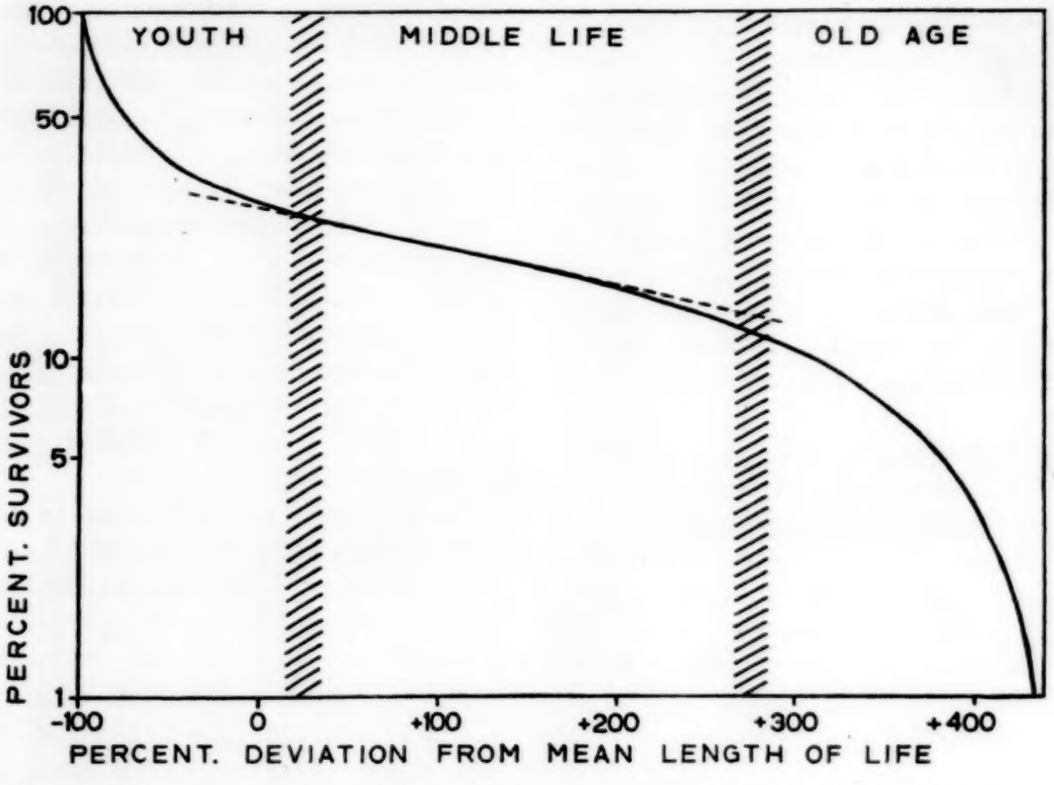

Fig. 1. Generalized survivorship curve, showing changes in rates of mortality during the life history of a cohort. This curve is based on a sample of *Stegodon* spp. (see text), but it is intended to demonstrate a general pattern of survivorship rather than a specific case. The dashed line is tangential to the curve at the point of inflection and indicates minimum rate of mortality in middle life.

far as we know, the corresponding part of the survivorship curve will in general approach a straight line, or form a gentle curve, slightly convex or possibly concave. Towards the termination of potential longevity, however, the relation between the organism and its environment is gradually altered by senescence; rates of mortality will ultimately be increased, if the population is large enough, or rates of mortality low enough, to permit some survivors to reach old age; and the curve will terminate with a downturn. Thus three main cycles may be discerned in the life history of a cohort: youth, with high but decreasing rates of mortality (survivorship curve concave); middle life, with relatively low and stable rates of mortality (curve more or less straight); and old age, with rapidly increasing rates of mortality (curve convex). These are illustrated by figure 1.

Age and Selection

In the life history of a cohort, selection begins at fertilization and ends at termination of reproductive capacity, except in some social forms where non-breeding members may be of importance in intergroup selection. Ultimately definable as the factor controlling differential reproduction, selection to a large extent works by differential mortality; and this is the aspect that may be illustrated by population dynamics.

The initial harvest of mass deaths in "prodigal" (Deevey, *op. cit.*) species may to a great extent be non-selective; but this, as Huxley (1942) has pointed out, does not invalidate the selection principle from holding for the remaining fraction. Thus it involves the weeding out of lethal combinations and many semilethals; it may affect the nursing facilities of the race, and so on; and, finally, many factors of preeminence in later life may enter the stage very early. In population dynamics this phase is usually the least well-known one, most estimates of juvenile mortality being formed from inference and not from observation. Much work will be needed before the emergence of a true picture of natural selection among juveniles.

Regarding selection during middle life, a great variety of topics suggest themselves; at present I only wish to point out that, long ago, Bumpus (1898), Weldon (1901), and di Cesnola (1907) have outlined methods for the study of centripetal selection of phenotypes. Another aspect will be treated below, in connexion with phyletic growth.

In the last stages of life, selection will have no influence on the gene pool of the population, if the old individuals do not breed any more (with the exception previously noted). Many forms seem however to be fertile to the end of their natural potential longevity. Thus the longevity of many mammals in nature seems to be determined simply by the condition of their teeth, which may be worn out when the animals are still physically in their prime (Flower, 1931). In the phraseology of Pearl, exogenous senescence is substituted for endogenous. This was seemingly the case with most of the Pliocene mammals studied by me, as the wear of their teeth was very rapid. The evolution of hypsodonty must be examined in this light.

Thus, the two ovibovines, *Plesiaddax depereti* Schlosser and *Urmiatherium intermedium* Schlosser, almost similar in gross size, differed markedly in hypsodonty: e.g. for M^3 the (mean) indices of hypsodonty,

$$I_h = \frac{100 \times \text{metacone height}}{\text{coronal length}}$$

are 102 and 127, respectively. Mean annual wear of this tooth was however proportional to gross size and not to crown height, being, in percentage of coronal length, about 18 for both forms.

Fig. 2 records the survivorship curves for these forms, from 2.5 years of age. Evidently the natural potential longevity of the more hypsodont *Urmiatherium* exceeded that of its ally; and, as a fairly large fraction of the cohort survived to this

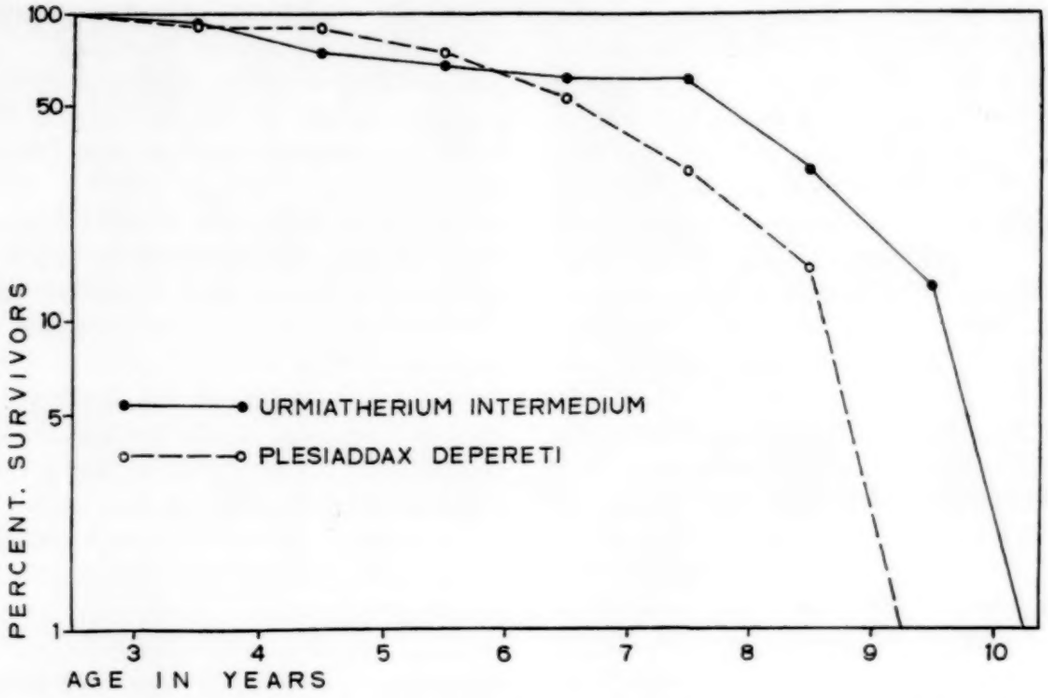

FIG. 2. Survivorship curves for the Pliocene Chinese ovibovines, *Urmiatherium intermedium* and *Plesiaddax depereti*, as labelled, from 2½ years of age. The higher natural potential longevity of the former is interpreted as dependent on degree of hypsodonty.

crucial age in both populations, and there is every reason to suppose that the oldest individuals were physically fit to reproduce, this factor should not be devoid of selective importance.

As to the variation within populations, the standard deviation of the hypsodonty index in *Plesiaddax* is 5.3, which would seem to result in considerable intrapopulation variation as to potential longevity. Under such circumstances, contrary to the opinion of Stirton (1947), a selective importance of this character would seem to be evident. It would indeed be hard to explain progressive hypsodonty in any other terms.

If the face of selection is thus changed during the life history of a cohort, so, it may be inferred, is its strength and effectiveness. From the studies of population geneticists we know that the effectiveness of selection is dependent on the size of the population. Hence, when a cohort is decreased in numbers with increasing age, the effect of selection will be diminished, and characters favourable in the young may be selected for even where they are to the detriment of the old (see Simpson's discussion of *Gryphaea*, 1944). This effect should be specially important in cases of diagonal survivorship, and will then be enhanced by the fact that the older age groups form a very small fraction of the total breeding population.

PHYLETIC GROWTH: RATES OF MORTALITY

Some data on mortality during middle life in mammals plainly bear on the problem of phyletic growth. This is apparent if the average adult rates of mortality for mammals of different size are compared. These average rates, which may be found by fitting a straight line as accurately as possible to the middle part of the survivorship curve (e.g. as in fig. 1), are inversely related to the size of the animal; or, in other words, there is a positive correlation between gross size and survival. For some extinct populations these rates have

been estimated as follows (from Kurtén, *op. cit.*):

Species	Average annual rate of mortality (in per cent)
Gazella dorcadoides	33.5
Ictitherium wongii	20.7
Plesiaddax depereti	14.3
Urmiatherium intermedium	10.4

To these may be added, as a preliminary result of a study of 55 mammoth molars in various Scandinavian museums, an estimate of between 2 and 4 per cent annually in *Elephas primigenius*. A similar value, 3 per cent, is indicated by a sample of *Stegodon* spp. (fig. 1; data from Colbert, 1943; Colbert and Hooijer, 1953); this latter sample may however be biassed.

For some recent mammals similar data have been computed, as follows:

Species	Average annual rate of mortality (in per cent)
Peromyscus spp.	96
Rupicapra rupicapra	24.8
Ovis dalli	8.3

These are based on data from Blair (1948, deermice), Bourlière (1951, chamois), and Deevey (1947, Dall sheep).

It is difficult to find any satisfactory measure of gross size for the fossil and recent forms. I have selected the length of the skull, which is available in all cases, in contrast with such *per se* more desirable parameters as total length or net weight. When rates of mortality or survival are plotted (arithmetically) against skull length (logarithmically), a fairly close interrelation appears, which may possibly be graduated by means of some sigmoid curve such as the logistic in figure 3. The proboscidean datum, which was not included in the graduation, is seen to agree well with expectation.

There is thus some evidence that rates of mortality and survival in adult mammals are more or less closely related to gross size. That this may be a potent factor in phyletic growth can hardly be denied, and indeed the concept is verbally formulated by Simpson (*op. cit.*). A

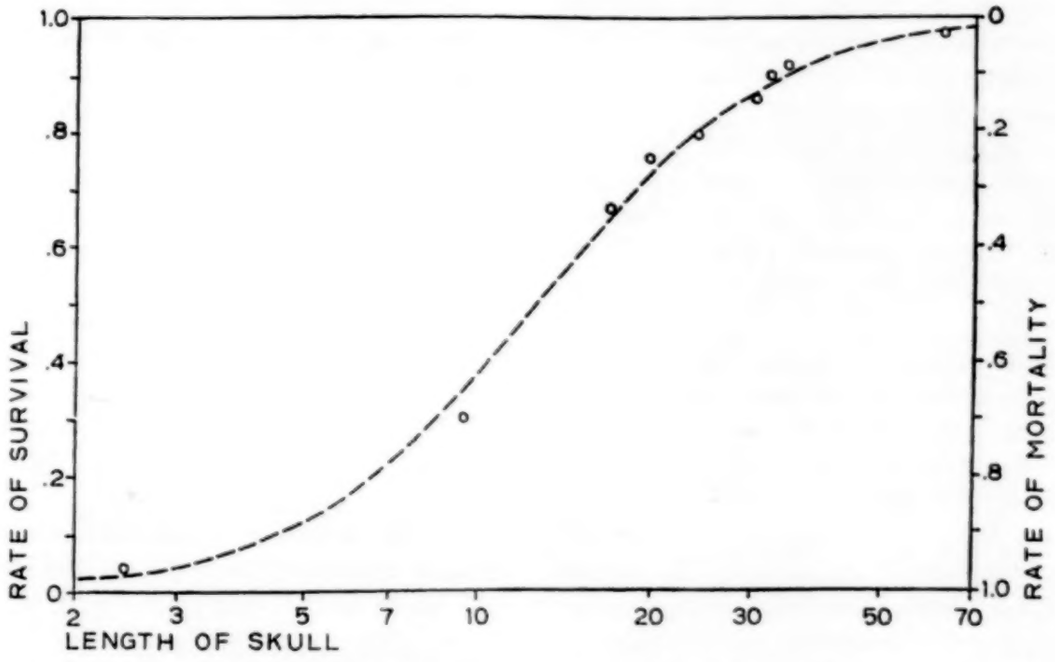

FIG. 3. Average middle life mortality and survival per annum for some mammals, plotted against length of skull (abscissa, logarithmic scale) as a rough measure of gross size. In ascending order of gross size and survival rate the forms are: *Peromyscus* spp.; *Lepus americanus; Gazella dorcadoides; Rupicapra rupicapra; Ictiterium wongii; Plesiaddax depereti; Urmiatherium intermedium; Ovis dalli; Elephas primigenius.* A logistic curve fitted to the data except the mammoth (Kurtén, 1953) is seen to describe the relation fairly well.

similar conclusion is reached by Newell (1949) regarding phyletic growth in invertebrates; population dynamics only can furnish the necessary evidence.

It should however be pointed out that the relation does not hold for mammals in radically different ecological spheres: thus, rates of mortality in bats are very much lower than those in terrestrial mammals of similar size (see Pearson *et al.*, 1952). Such differences may obviously exist on lower levels of ecological differentiation too. Finally it should be mentioned that even in the same species, rates of mortality may fluctuate from place to place (see Farner, *op. cit.*) as well as from time to time.

Some Additional Factors of Phyletic Growth

By increasing the area under the survivorship curve, or, in other words, by increasing the potential possibilities for reproduction, diminished rates of mortality have an apparent selective advantage. A similar result is attained if the potential longevity is increased, provided that the reproductive capacity remains unimpaired and the interval between successive breeding seasons is not prolonged. The special case of progressive hypsodonty has been discussed previously. That phyletic growth may have a similar effect is pointed out by Rensch (1947): "Ganz allgemein werden grössere Warmblüter älter."

If, for instance, the averages of longevity records for mammals in captivity are plotted against some measure of gross size, for a limited taxonomic group (e.g. a family), the dependence will be seen to conform fairly well with the "allometric" curve (see Kurtén, *op. cit.*). This regression is not identical in different taxonomic groups, but the tendency would seem always to favour size increase.

Another possible factor of phyletic growth of special interest to population dynamicists, discussed e.g. by Rensch (1947) and Petersen (1950), is the difference in output of young between size variants in cold-blooded animals. The relation has been graduated for some populations by Petersen (*op. cit.*, spiders) and Kurtén (*op. cit.*, crustaceans), and is, similarly, allometric in pattern.

Inhibitions to Phyletic Growth

Obviously, not all animals are giants; and it is evident that the trend towards size increase must in general be countered by opposing agencies. From the point of view of population dynamics, one important limit to phyletic growth in mammals may be conditioned by the relation between gross size and length of gestation. This relation, again, is of an allometric pattern, and differs for different taxonomic groups, but is usually clear-cut and close (see Kurtén, *op. cit.*). In seasonally breeding forms, such as most larger mammals, gestation periods approaching one year in length would obviously be disadvantageous, since this would delay or prohibit next year's breeding and thus diminish the output of young. Accordingly, we find that very few mammals have gestation periods exceeding the limit, whereas many species (in particular large Bovidae) are "crowding" immediately beneath it. There seems here to be an evolutionary threshold, which might be traversed, either by a radical change in breeding habits, or by quantum evolution.

This limit, however (along with the physical and physiological limits, which are not considered here), will not assume importance until at a late stage of phyletic growth. The majority of mammals are well beneath the threshold, and, moreover, phyletic dwarfing is known to have occurred.

The factor inhibiting phyletic growth or actually reversing the trend would in general seem to be selection for a specific niche, where a certain gross size is optimal; possibly this influence may be enhanced by intergroup competition from the form occupying the "next larger" niche. Thus gross size would in general be a fairly stable character, as indeed it appears to be. The normally repressed

selective growth factors may, however, offer a possible "released spring" mechanism, when the inhibiting agency is removed. They would thus exemplify selection of a nonadaptive or preadaptive, rather than strictly adaptive nature, curiously reminiscent of the orthogenetic and related concepts of inner urges and the like. No universal validity is claimed for this hypothesis, but it might account for some instances of fast-evolving gigantism, and for lineages where phyletic growth is found to proceed in a jerky fashion.

Conclusions

This has led somewhat far into the realm of speculation. The dynamics of natural populations is however (to say the least) a newfledged science; and its evolutionary implications have not yet received full attention. One important deficiency is easy to discern: the problems cannot as yet be posed in genetical terms. Wood (1947) made the very attractive suggestion that attention in paleontology and genetics be focussed on rodents, as rendering possible a tie-in between these sciences. Similarly, rodent ecology is now being very widely studied, and it may well be that the future synthesis will be built, to a large extent, on rodent research. Certainly it may be said that the problem of survival is a central one in this integration, and that no theory of selection will be complete unless it states *when* and *how*, in the life history of a cohort, selection operates.

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NOTES AND COMMENTS

REVISION OF THE FLORISSANT FLORA [1]

DANIEL I. AXELROD

The Florissant lake beds, situated in central Colorado at an elevation of 8500 feet, are well known for the great wealth of fossil plants and insects they contain; scarcely a textbook of historical geology has failed to devote at least a paragraph to this richest Middle Tertiary deposit of North America. Although over 40 papers have been writtern about the flora, the only comprehensive report has been that of Leo Lesquereux, published over 70 years ago. The appearance of a complete revision of this well-known, yet up-to-now relatively little understood flora, is therefore particularly welcome.

MacGinitie has spent fully a decade of intensive work unravelling the geology, the composition, the paleoecology, the age, and the relationships of the Florissant to other Oligocene floras in North America. Some of his major conclusions are herewith summarized:

Geologic occurrence. The Florissant beds are erosion remnants of Oligocene fluvatile and lacustrine sediments associated with chiefly andesitic pyroclastics. They were laid down on a piedmont at the east front of the ancestral Rocky Mountains, at an elevation of probably not more than 3000 feet. Relief was generally low, with wide valleys and low, rolling divides between the streams. Higher terrain lay to the west, where volcanic cones rose a few thousand feet above the site of deposition. Owing to an exceptionally favorable topographic setting, with lakes and ponds adjacent to active cones, ash showers were highly effective in rapidly burying and preserving numerous plant and insect remains in the fine-grained shales.

Composition. Although 250-odd plants have been described from Florissant, MacGinitie recognizes only 114, of which 19 are described as new from his large collections. Thus only about 30 per cent of the original species are retained, and nearly half of these have referred to new genera. The drastic nature of the revision is emphasized if we note that MacGinitie includes a list of synonyms 10 pages long. In view of this critical revision it is readily understandable that the flora has not been properly understood up to the present time. MacGinitie points out that nearly 60 per cent of the plants have similar living equivalent species in the region a few hundred miles to the south and southeast, where 3 different modern floras—the Ozarkian-Appalachian, the southern Rocky Mountain, and dry subtropic Mexican—intermingle today in areas of moderate relief. Approximately 30 per cent of the plants have their nearest modern relatives in the warm temperate parts of eastern and southeastern China, with the remainder scattered in western North America and South America.

The flora represents an ecotone between the temperate Arcto-Tertiary Flora which migrated southward across holarctica during the Tertiary, and the semiarid Madro-Tertiary Flora which had an autochthonous origin in southwestern North America and spread radially over that region during the Middle and Later Tertiary. The associated insect fauna displays similar relationships, being a mixture of temperate and dry subtropic (or warm temperate) genera.

Paleoecology. A rich mesic forest of Arcto-Tertiary derivation occupied the stream- and lake-borders in the broad valleys, having extended into the lowlands from the cooler slopes of volcanos to the southwest. This community included species of *Acer, Carpinus, Carya, Celastrus, Chamaecyparis, Crataegus, Halesia, Hydrangea, Koelreuteria, Lindera, Malus, Osmanthus, Populus, Quercus, Rhus, Robinia, Salix, Sequoia, Staphylea, Tilia, Ulmus, Vitis* and *Zelkova.* A few rarer plants, in such genera as *Abies, Pinus* and *Picea,* appear to have lived on more distant, upland slopes. Interfluvial areas over the lowlands, characterized by better drainage and more frequent and persistent drought conditions, supported an evergreen live oak woodland and savanna and their associates of Madro-Tertiary origin. The live oaks (4 species) intermingled with *Bursera, Caesalpinites, Cardiospermum, Celtis, Cercis, Colubrina, Conzattia, Euphorbia, Platanus, Prosopis, Prunus, Sapindus, Thouinia* and *Vauquelinia* along stream courses. A number of these plants probably formed a thorn forest, much like the present-day Tamaulipan scrub, in the drier washes. A chaparral, including species of *Dodonaea, Cercocarpus, Mahonia, Quercus* (scrub oak), *Rhus, Schmaltzia* and *Zizyphus,* occupied dry exposed slopes. Mesquite grassland probably was well developed over the drier parts of the interfluves.

Judging from the structural characters (leaf size, texture, etc.) of the leaves, the climatic implications of the rich insect fauna, and the climatic relationships of modern vegetation most nearly like the flora, MacGinitie concludes climate was warm temperate, with an annual rainfall of from 20 to 25 inches, concentrated

[1] MacGinitie, Harry D., Fossil plants of the Florissant beds, Colorado. Carnegie Inst. Wash. Pub. 599. 188 pp. 75 pl. 1953. $5.25 paper bound; $5.75 cloth

chiefly in the summer half of the year. Annual average temperature was not less than 65° F., the absolute minimum temperature probably was not below 20° F., and the average temperature of the warmest month approximated 80° F. Such conditions recall those near Monterrey, Mexico, today.

Age. Following their extensive studies of the flora, the insects and the fishes during the late seventies and early eighties, Lesquereux, Scudder and Cope all regarded the Florissant beds as Oligocene in age. In more recent years, Cockerell, Knowlton and Berry have considered the Florissant as Late Miocene. After carefully reviewing the stratigraphic, floristic and fragmentary mammalian evidence, MacGinitie concludes the Florissant beds span the Lower to Middle Oligocene, with the flora representing the later part of Lower Oligocene time. MacGinitie's review of the Oligocene floras of the United States is welcome for it emphasizes the provinciality of vegetation at this time. As he points out, the floras of the Pacific Northwest, the central Rocky Mountain area, and the Gulf and south Atlantic Coasts, are widely different in character and local differences are apparent in each province.

MacGinitie's sound paleobotanical work is well recognized, and this volume will stand as one of his more significant contributions. It can easily serve as a model for workers monographing other angiosperm floras. His results, drawn from a critical synthesis of geologic, botanic and climatic data, only serve to emphasize again the ineptitude of most of the earlier workers in the field.

The Florissant volume is well written and well printed, the 75 plates are excellent, and it is remarkably free from typographical errors. It stands as a tribute to both the author and the editorial staff of the Carnegie Institution of Washington.

HOW MANY SPECIES?

André Cailleux

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In a short, but very fine paper, G. G. Simpson (1952) tried to guess how many species lived since the beginning of life on the Earth until the present day. I wish to attack here the same problem, but in a somewhat different way.

From the comparison of several lists of fossils, originating from different places and geological ages, but being of the same facies (in other words: of the same kind of biotope and thanatotope), I have shown, both from littoral marine shells (Cailleux 1950) and aerial plants (Cailleux, 1952), that the number of species simultaneously present (exactly: preserved) in one place, increased during the geological times, approximately and meanly according to a geometrical progression. I presumed that the same law applied to all living beings; the number of species seems to have doubled every A = 80,000,000 years. The living species described at present being about 2 millions in number, and the existing ones, 4 millions, the origin of life would have been about 1,700,000 to 1,800,000 years ago which is in good accordance with Simpson's estimate of 1,000,000 to 2,000,000). Knowing the species mean duration E, it is easy to calculate the total number N_t having existed in the whole history of life. We have:

$$N_t = N_v \frac{A}{E \log_e 2} = 1{,}44\ N_v \frac{A}{E}$$

These guesses can be used as follows:

	Guesses leading to estimate that are:		
	Maximal	Medial	Minimal
Present day living spp. N_v	6,000,000	4,000,000	2,000,000
Time of doubling A	100,000,000	80,000,000	60,000,000
Mean duration of spp. E	1	3	10
Total species $N_t = 1{,}44\ N_vA/E$	860,000,000	150,000,000	17,000,000
Total species Acc. to Simpson	4,000,000,000	341,000,000	50,000,000

There is a good accordance between Simpson's results and my own. Only mine are about 3 times lesser. If they are true, it means that, of all the species having ever lived, the paleontologists know, or have the hope to know, a percentage 3 times greater than even G. G. Simpson guessed.

I wish to thank my friend J. M. Chevallier for his kind help.

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SIMPSON, G. G. 1952. How many species? Evolution, 6: 342.

EXPERIMENTAL BIOLOGY AND EVOLUTION [1]

EVERETT C. OLSON

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In a recent symposium, a number of students of experimental biology have cooperated to produce a series of 22 reports on evolution from the viewpoint of the experimentalist. They have delved deeply into matters that are of common concern to all who are interested in evolution. The subjects are so varied and many are so stimulating that this volume becomes "required reading" for the student of evolution. The words of J. S. Haldane, in the final paragraph of his foreward, catch the underlying impression that your reviewer, at least, gained from these studies: ". . . a number of workers are groping from their own different standpoints toward a new synthesis while producing facts that do not fit well into the commonly accepted synthesis. The current instar of evolutionary theory may be defined by such books as those of Huxley, Simpson, Dobzhansky, Mayr and Stebbins. We are certainly not ready for a new moult, but signs of new organs are, perhaps, visible. The papers here collected represent points of view too divers to be capable of co-adaptation at present. They certainly achieved less unity than did the symposiasts at Princeton. This is not a bad sign. It points forward to a broader synthesis in the future."

The volume opens with a vigorous excursion into a new hypothesis on the origin of life by J. S. Pringle.[2] Life is conceived to have developed in the stagnant parts of the deep sea. Like other hypotheses concerning the non-living precursor of life and the transition to living matter, this one will raise grave doubts in the minds of many readers, but it can hardly fail to be stimulating. The hypothetical scheme involves branching chain reactions and calls into play important known aspects of physical chemistry. Special sets of coincidental phenomena are not essential under this hypothesis. It is an important point that some phases of this concept are subject to experimental testing.

With the stage set by this departure into hypothesis, the following contributions present an impressive array of data, interpretations and suggestions that are, for the most part, not inhibited by any evident effort to fit them into the present day synthesis. A number of papers, perhaps ten in all, have genetics as their principal concern. It is significant that more than half of these include both ecological and ethological considerations, pointing to the increasing need of coordination of different fields of study. K. Mather,[3] presents a concise account of the genetical structures of populations, which, for the most part, is consistent with the views of the majority of present day students. This is a stabilizing influence in a series that frequently departs from this general frame of reference. Genetics in closely related species, subspecies or races are considered in four separate papers by H. G. Baker,[4] D. H. Valentine,[5] D. M. Stevens,[6] and H. Spurway.[7] Just how important these detailed analyses will prove in evolutionary study may eventually be solved by more such studies and an extension of their results to test the validity of the concept that speciation and the development of subspecies are dominant factors in evolution. At present, evaluation seems to

[1] Symposia of the Society for Experimental Biology, VII: Evolution. Academic Press Inc., New York, N. Y., 1953; 440 pages. $7.80.

[2] The origin of life, pp. 1–21.

[3] The genetical structure of populations, pp. 66–95.

[4] Race formation and reproductive method in flowering plants, pp. 114–145.

[5] Evolutionary aspects of species differences in *Primula*, 146–158.

[6] Recent evolution in the genus *Clethrionomys*, pp. 310–319.

[7] Genetics of specific and subspecific differences in European newts, pp. 220–238.

lie largely in the realm of individual evaluation of rather fragmentary evidence.

Those who have followed the recent work of C. N. Hinshelwood will find a valuable summary in his report on adaptation in micro-organisms[8]. As an introduction to his experimentation and conclusions, the paper may prove a strong dosage and the full import may be missed in a first reading. The process of bacterial adaptation, which is shown to occur rapidly and to result in changes that persist, is considered in some detail as an automatic development of rudimentary potentialities. There is a clearly drawn line between the "adaptationist" and "selectionist" points of view, and, whether the evidence is considered definitive or not or whether the concepts are incompatible or not, the careful consideration of the postulated autocatalytic medium of change given by the writer provides a basis for sane discussion of this area of controversy.

The paper of M. Demerec,[9] which considers the reactions of certain bacterial genes to mutagens, is complementary to the report of Hinschelwood. Analyses are in a more generally accepted framework and of great interest from a biochemical point of view. How much either of these papers has to do with major aspect of evolution, and how and why bacteria evolve still appears to be an open question. A stochastic approach to the growth of bacterial colonies and bacterial mutation is offered by D. G. Kendall.[10] The increasing use of stochastic models in the biological sciences accords particular interest to this work. The skeptical will point to over-simplification, the necessity for limiting postulates, and the difficulty of supplying data for even mathematically simple models. Perhaps some bold synthetist may consider the possible interrelationships of the studies of Kendall, Demerec and Hinschelwood.

C. H. Waddington's[11] concise consideration of epigenetics and evolution stresses the distinction between "normalizing" and "stabilizing" selection. His important work in epigenetics is not unfamiliar to the readers of EVOLUTION and need not be elaborated in this review. A particular challenge to evolutionists is offered by his suggestion of three major fields of inquiry most needing attention: (1) the problems of adaptation, (2) the nature of differences between species or species groups, and (3) problems of "long range evolution in time" posed primarily by paleontological materials.

A study of cytological evolution of the ferns of Ceylon by I. Manton[12] contains the most interesting conclusion that "evolution must be proceeding faster in the tropics than in temperate latitudes." The opportunity for recolonization of ecological sites appears to be an important factor and the continuing opportunities for such events in the tropics over long periods appears to be documented in Ceylon. Recession of the glaciers during the Ice Age in Europe probably presented unusual opportunities of this sort, but the very fact that they are unusual, and temporally limited, suggests that they were of only passing significance. Another paper concerning evolution in a special environmental province, also tropical, presents Holttum's detailed analysis of evolutionary trends in an equatorial climate, based on work in Singapore.[13] Uniform climate has permitted the evolution of plants that are continuous in growth and flowering. But, strikingly, there also have arisen plants that respond to peculiar and slight climatic stimuli. Some, but not all, desiduous trees, on the contrary, show a rhythmical behavior that is independent of climatic stimuli. The contrast between the environmental opportunities detailed in these two studies is great and must be a constant reminder of the danger of generalities based on a broad concept such as "tropical environment." Certainly in this case, there are common factors, but the evolutionary aspects of the floras seem best explained in terms of the different characteristics of the local environments.

Three reports, contributions by W. Hovanitz,[14] and P. M. Sheppard,[15] and W. H. Dowdeswell, and E. B. Ford,[16] deal with polymorphism and evolution in the Lepidoptera. Perhaps the most striking insight that comes from these studies is the great difficulty of analysis, in even relatively simple evolutionary situations where polymorphism is an expression of gene frequency, in spite of the fact that a great deal may be empirically determined concerning populations. Such studies of structure as related to polymorphism in wild populations provide a type of searching study and interpretation necessary to expansion and reinterpretation of more highly theoretical population studies, based on mathematical considerations and on laboratory experiments with controlled populations.

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[8] Adaptation in micro-organisms and its relation to evolution, pp. 31–42.

[9] Reaction of genes of *Escherichia coli* to certain mutagens, pp. 43–54.

[10] Stochastic processes and the growth of bacterial colonies, pp. 55–64.

[11] Epigenetics and evolution, pp. 186–199.

[12] The cytological evolution of the fern flora of Ceylon, pp. 174–185.

[13] Evolutionary trends in an equatorial climate, pp. 159–173.

[14] Polymorphism and evolution, pp. 238–253.

[15] Polymorphism and population studies, pp. 274–289.

[16] The influence of isolation on variability in the butterfly *Maniola juritina* L., pp. 254–273.

E. Baldwin [17] and P. B. Medewar [18] separately treat problems that involve biochemistry and evolution. The place of biochemistry is becoming increasingly important in evolutionary studies as new unities at the molecular level are unveiled, and the existence of previously unknown continuities in organic systems is revealed. Baldwin cites examples of the use of biochemical constituents in recognition of major evolutionary relationships, whereas Medewar treats a specific, although broad, situation with respect to immunological and endocrinological problems in the evolution of viviparity in vertebrates. From a detailed discussion of a most complex problem, arises the important generalization that "endocrine evolution is not an evolution of hormones but an evolution of the uses to which they are put." This is an evolution of reactivity and one is tempted to draw analogies between Medewar's concept of 'endocrine evolution' and concepts of evolution of reactivities at other organizational levels throughout the complex that is the organism in ontogeny and the super-individual complexes in which organisms are associated in evolution.

The evolution of structure is the basic theme of two papers, one by S. M. Manton,[19] on the locomotor habits and evolution of larger arthropods, and the other by E. M. Willmer,[20] on determining factors in the evolution of the retina. The study of S. Manton is a survey and analysis of the evolution of a functional system, in a phylum, that relates morphology to function and considers the evolutionary impact of the association. As such, it is outstanding and should stir the thoughts of the paleontologists who may tend to feel remote from experimental work. E. N. Wilson places particular emphasis upon the concept that the most likely course of evolution in the optic structures of vertebrates is condition by the limited types of cells provided the optic organ in the embyro. It will, thereby, be the course that provides the greatest advantage in the use of these cells for the particular type of animal possessing them. Eyes are, so to speak, bound to be variants on a set theme. Once the pattern of development from the optic vesicle of the neural tube was established, the ramifications and potentialities for vertebrates were set within certain limits. The limitation of potentialities is also stressed, on a somewhat different basis, by S. Manton. This concept constantly arises in consideration of the evolution of major groups of animals and organic systems. In notable instances, it has given rise to the feeling that evolution is in essense a restrictive process and has reached, or nearly reached, an end. This is certainly not the import of the conclusion reached by these two authors, but the basis for argument is offered.

Fitness is a common problem in most studies concerned with evolution. J. M. Thoday [21] has offered a provocative discussion of the components of fitness that deserves careful attention. The fitness of a contemporary unit of evolution, which ranges from an apogamus individual to a super-specific group with the potential of hybridization, is defined as the probability of such a unit leaving descendants. Biological progress is the increase in such fitness. Stress is given to the antagonism between genetic stability and flexibility and phenotypic flexibility, a component of variability that is independent of genetic flexibility. Some of the questions that Thoday raises are fundamental. We cannot but be a bit dismayed at the thought that fitness in a specific situation requires a period of some millions of years for a test of judgment. The need for some unit for evaluation is evident in most evolutionary studies. Just what unit is to be used must depend in large part upon the nature of the problem and what is available for its study. Perhaps Thoday's unit is the best for his purposes, and possibly in theory for others as well. Regardless of what evaluation may be put on his conclusions, there is little doubt that this article fulfills its (apparent) major objective, to stimulate thought and to provoke discussion.

A study by M. J. Heuts [22] on regressive evolution of cave animals has already found its way into the pages of EVOLUTION, through a review by C. M. Breder [23] and a subsequent reply by Heuts.[24] The paper is certain to evoke additional controversy, for it is full of interesting ideas, which frequently depart from more usual interpretations. The report must be read *in toto*, if the comments that EVOLUTION has carried are to be judged in proper perspective.

The part that social behavior has played in the evolution of primates is the subject of the final paper of the symposium. While behavior patterns are considered elsewhere in the volume in their relationship to evolution, the importance which they are accorded by M. R. A. Chance and A. P. Mead [25] in the closing paper is unique.

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[17] Biochemistry and evolution, pp. 22–30.

[18] Some immunological and encocrinological problems raised by the evolution of viviparity in vertebrates, pp. 320–338.

[19] Locomotory habits and the evolution of the larger arthropods, pp. 339–376.

[20] Determining factors in the evolution of the retina in vertebrates pp. 377–394.

[21] Components of fitness, pp. 96–111.

[22] Regressive evolution in cave animals, pp. 290–311.

[23] Cave fish evolution, C. M. Breder, Evolution, 7: 179–180, 1953.

[24] Comment on "Cave fish evolution," M. J. Heuts, Evolution, 7: 391, 1953.

[25] Social behavior and primate evolution, pp. 395–431.

Social behavior is considered a primary factor in man's evolution, although not presented as a complete explanation of man's evolution; rather, in the words of the authors: ". . . the ascent of man has been due in part to a competition for social position, giving access to the trigonal sphere of social activity in which success was rewarded by a breeding premium, and that at some time in the past a group of primates by virtue of their pre-eminent adaptation to this element and consequent cortical enlargement, became pre-adapted for the full exploitation of the properties of the mammalian cortex." Much that is considered in this study is unusual in evolutionary literature and some of it may seem trivial unless read in context. The case for the importance of social behavior patterns as a primary factor in primate evolution necessarily rests in part on speculative considerations. Certainly, insofar as behavior patterns of the type discussed are unique among primates and have undergone a "phylogeny" of the sort suggested by studies of extant primates, they may be presumed to have had a role in the evolution of this order. How important this role may have been is the matter of controversy. Chance and Mead offer a strong case for their point of view.

No adequate summation of the contents of this volume can be made. For each item to which attention has been directed in the foregoing paragraphs, there are several that might also have been noted. Some papers are specifically based on experimentation, others partially so, and some, strictly speaking, are non-experimental. No reader should pass the book by because his interests have only a remote or indirect relationship to experimentation. There is something for everyone interested in evolution and a great deal for most.

THE MAJOR FEATURES OF EVOLUTION [1]

EVERETT C. OLSON

As originally conceived, this new study of evolution by George G. Simpson was to be merely a revision of Tempo and Mode in Evolution.[2] The modifications in fact are so extensive that they go far beyond a simple revision to produce what in many respects, is a completely new book. The basic framework, however, is preserved and the subject matter, although expanded, modified, and illustrated by a wealth of new material, is roughly the same as that of Tempo and Mode. It will not be necessary to give a detailed account of the coverage or the way in which the materials are brought into perspective under evolutionary theory, since most of the readers of EVOLUTION are well acquainted with Tempo and Mode.

This book offers a mature statement of what its writer terms the "synthetic theory" of evolution. The factors emphasized are those considered most essential to evolution from the standpoint of "four dimensional" biology, for no attempt is made to review the whole field of evolution from all points of view. As in the earlier book, particular emphasis is accorded the subject of rates of evolution, three chapters being devoted exclusively to this field of study. Specific consideration of modes of evolution is confined in large part to the short final chapter of the book. Throughout the whole treatise, population concepts provide a fundamental basis for integration of the highly diverse array of ideas and materials. The result is a coherent, readable and appealingly unified concept of evolution that will certainly find favor with the majority of students of evolution today.

The challenge of speculation and originality characteristic of Tempo and Mode is largely absent from this new book, for the intervening years have seen a great increase in knowledge and a solidification of many of the concepts tentatively advanced about a decade ago. Where earlier ideas have proven in error or misleading, changes have been made, but for the most part criticisms have been ably dealt with without major revision of the concepts that were under fire. Rather, there have been modifications of emphasis and reconsiderations of the relative importance of related phenomena. The solidity of the study is welcome, but your reviewer, at least, cannot but feel small twinges of nostalgia for the "brave new world" approach of the earlier volume and a vague uneasiness of false security in the niceness with which the interrelated factors mold into a coherent unit. If the reader recognizes, as Simpson most certainly does, that new facts about evolution that may or may not fit the synthetic theory are constantly being uncovered and that this book is the statement of a point of view, the possible dangers always inherent in the crystallization of a particular framework will be avoided.

Seven items are listed by the author as "the factors most likely to cast light on major aspects

[1] The major features of evolution, George G. Simpson. Columbia University Press, New York, N. Y. 1953, pp. 434. Price $7.50.

[2] Tempo and mode in evolution, George G. Simpson. Columbia University Press, New York, N. Y. 1944, pp. 237.

of evolution, . . ., and to relate them to the primary evidence of long-range evolution": 1) variation, 2) mutation, 3) population, 4) time and length of generation, 5) selection, 6) environmental factors, and interaction of all factors in adaptation, and 7) isolation and splitting. Each of these factors is considered in detail, more or less in this order. It is emphasized, however, that any division of factors, necessary as it may be for discussion, is artificial and that the interplay is what in fact determines the course of evolution.

There are many sections of the book that call for an extended commentary, too many for inclusion in a short review, but two concepts, in particular, demand special mention. One concerns the application of the population concept to extinct organisms. Simpson, probably more than any other person, has been responsible for recognition of the importance of this approach among paleontologists and thereby has rendered a signal service. The power of the concept is exemplified in the chapter entitled "Population and Selection" in which its various facets are widely explored. So long as the idea of the population is considered in general terms and analogy with modern populations is used as a primary basis for interpretation, no serious difficulties arise in studies of fossil samples, and it is at this level that Simpson pursues his considerations. When, however, we wish to examine the details of extinct populations, whether *demes*, species, or interspecies, very real difficulties arise in the estimation of such features as population size, population structure and dynamics, or the form of frequency distributions, which is so important in the interpretation of statistical parameters. These problems are not raised in the book except in rather brief reference to population size as it pertains to species.

The second matter of particular importance concerns organisms and their relationships to their environment. This relationship is considered throughout the book and is given particular emphasis on chapters VI and VII which deal with "Adaptation" and "The Evolution of Adaptation." Here the nature and significance of adaptive zones and the adaptive grids, presented rather briefly in Tempo and Mode, are analyzed in detail with a welcome increase of illustrative materials. The stage for a consideration of such topics as trends, orientation, extinction and modes of evolution is set in these chapters. Morphological adaptation is the focal point of interest. I cannot help but feel that the promise of the first few pages of the sixth chapter, in which the relationship of organisms and their environments is discussed, is never fully realized in the subsequent pages of the book. Perhaps it is inevitable, in view of a primary concern with the organisms, that ecological aspects of interrelationships of organisms and their integration into unified ecological systems remain secondary considerations. Possibly the writer does not consider that these relationships are of prime importance or, perhaps, he feels that the data available for extinct populations are insufficient for analysis. It seems difficult to conceive, however, a complete synthesis that does not give special emphasis to this aspect of the organic world which, in my opinion at least, is a fundamental factor in evolution. The differences of opinion in this respect probably stem from different points of view, the one which recognizes as central the position of some taxonomic unit in its environment, and the other which considers the interrelationships of suites of such units to each other and to their physical environments as primary. Some aspects of evolution that are rather awkwardly explained under the first point of view, major extinctions for example, appear to fall into a coherent and unified pattern under the second.

A final note is needed about the examples that are used throughout the book. Whereas Tempo and Mode included, of necessity, only relatively few examples, "The Major Features of Evolution" is replete with illustrative materials drawn from a wide variety of fields. The author, to paraphrase his own statements, suffered in selection from an embarrassment of riches. The work during the last decade, in part stimulated by Tempo and Mode, has been such that it is now possible to be reasonably selective in assembling pertinent examples for illustration of the operation of various factors of evolution. It is inevitable that a preponderance of examples from the fossil world will be drawn from the ranks of the mammals and that many of them will be concerned with teeth. This is a commentary on the fossil record and the interests and aims of students in various fields of paleontology, rather than upon the author's preference in the matter, for, in fact, the bias of his materials is less, probably much less, than the bias that would result from a tabulation of studies of evolution over the full array of major taxonomic groups. Nevertheless, it must be clear that generalizations are based on less than a fully adequate sampling of the organic world. Insofar as the principles and factors are common to all life, no difficulty arises. There is a high probability that this is the case for the great bulk of sexually reproducing groups. We can have somewhat less confidence that a synthesis based primarily on the studies involving one or a few characters or parts of organisms may not fail to include or to give appropriate emphasis to important factors that must at sometime take their place in the framework of the theory of evolution. This area of study, as well as others, is just now being brought into focus. Whether or not the facts that they may reveal will fit the current synthesis as portrayed by Simpson only the future can decide. Be this as it may, the task of integration or reformulation, as required, will be tremendously simplified by the clear statement and analysis with which Simpson has provided us.